A quantitative exploration of the meso-scale structure of ecological networks

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School of Biological Sciences
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Dedicated to my friends for their understanding

and support

Contents

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The candidate conducted the majority (>80%) analysis and most writing (>80%) associated with both the thesis chapter and the published work. Co-authors Kaartinen and Roslin provided data for analysis and advice about biological components for inclusion in the discussion. Co-Author Stouffer provided valuable guidance and discussion for the conception of the project and the data analysis. In addition, Stouffer provided invaluable writing help in the form of edits and general guidance.

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Name:	Signature:	Date:
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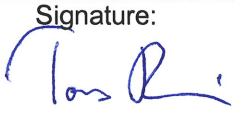
Riikka Kaartinen		May 18, 2015
TOMAS ROSLIN		May 18, 2015

Preface

This thesis has been written as two stand-alone scientific articles. The first, *"Species' roles in food webs show fidelity across a highly variable oak forest"* was published in *Ecography* February 2015: Volume 38, issue 2, pages 130–139. The second, *"A meso-scale approach to understanding macro-scale measures of ecological networks"*, we intend to submit to *Journal of Complex Networks*. Preceding these articles is a wider review of the relevant literature than is present in the introductions of the articles themselves. Finally, in *"Conclusions"*, we discuss the relevance of the two articles to each other, to the existing scientific literature, and to their application in ecology.

Abstract

Analysing ecological communities as complex networks of interactions has become an important tool for ecologists. Understanding how these networks change through time, over landscapes, or in response to disturbances is a primary goal of community ecology. The number of interactions and the way in which those interactions organise themselves as individuals, small groups, and the whole community can play an important role in predicting how ecological communities will respond to disturbances. In this thesis, we investigated variation in network structure at several scales both empirically and in a theoretical context.

Our first hypothesis was that the structural role of species in a variable system would show little variation, despite high levels of species turnover and a fragmented landscape. In a collaboration with Riikkaa Kaartinen and Tomas Roslin, we studied the distribution of species' roles at three scales in host-parasitoid networks collected from a fragmented forest in Finland. We found that species' roles were remarkably consistent through time and in the presence of species turnover. These results suggest that species' roles may be an intrinsic property of species and may be predictable over spatial and temporal scales.

Our second study investigated the structural variation of simulated ecological networks and the relationship between structural variation and whole-network measures of network organization, such as connectance, nestedness, and modularity. We quantified structural variation of networks at three scales, macro-scale, motif-scale, and participation scale. These scales represent whole-network measures (macro-scale), sub-network measures (motifs – small groups of interacting species), and individual measures (motif participation). We compared the variation in these structures to connectance, nestedness, and modularity. We found that at fixed levels of connectance, nested-

ness, and modularity, the motif profiles of networks and the distribution of species across those profiles showed remarkable dissimilarity. This result suggests that networks displaying similar macro-scale structural measures can be composed of vastly different motif- and participation-scale structures.

Together, the work that makes up this thesis suggests that we should give more attention to the meso-scale structures of ecological networks. As the more detailed perspective of motifs can capture additional detail about the structure of empirical networks, and as a result, provide a clearer picture of ecological communities. In addition, we found that the particular species themselves can have a significant impact on the meso-scale structure and, in some cases, may impose strict limitations on what interactions can occur within a community. This has important implications for our understanding of how ecological networks are built and maintained, and thereby for our understanding of the stability and resilience of ecological communities.

Introduction

We are currently experiencing a global biodiversity crisis due to an exceptionally high rate of species extinction (Pimm et al., 2014). Current extinction rates are estimated to be approximately 100 species extinctions per million species per year ($100E/MSY$) (De Vos et al., 2015; Pimm et al., 2014). This rate dwarfs the background extinction rate which has been estimated at $0.1E/MSY$ (De Vos et al., 2015). Furthermore, the current extinction rate only takes into consideration known species. There are still millions of unknown species, approximately 86% of land species and 90% of ocean species are estimated to be undescribed (Mora et al., 2011). Further, it is likely that these estimates don't appropriately measure the rate of extinction for rare species that have only recently been described (Lees and Pimm, 2015). In addition, regional extinction rates can be much higher than the global average (e.g., North American rivers and lakes are estimated to be at $954E/MSY$ and Africa's Lake Victoria has an extinction rate that exceeds $1000E/MSY$ for fish species (Pimm et al., 2014)). As a result, it is believed that the current rate of species extinction is actually an underestimate and that the real values are more severe (Pimm et al., 2014; De Vos et al., 2015).

There are a number of consequences related to the current rate of biodiversity loss. The loss of species from natural habitats can dramatically alter the composition, function, and resilience of ecosystems which, in turn, can directly impact human health and safety. The benefits of a diverse, fully-functioning, ecosystem include breathable air, productive fisheries, fertile grounds for planting crops, along with cultural and spiritual benefits (Millennium Ecosystem Assessment, 2005b). These ecosystem services are only attainable if the biodiversity of the ecosystem is in tact and is able to generate the necessary functional processes (Millennium Ecosystem Assessment,

2005a). Thus, changes to the composition and diversity of natural systems can alter the availability of food, sources of fuel and structural materials, and medicines both known and as yet undiscovered (Millennium Ecosystem Assessment, 2005b). For example, it is estimated that the value of undiscovered pharmaceuticals from plants in the tropics alone is $109 billion (Millennium Ecosystem Assessment, 2005b). In addition, the loss of species also leads to a loss of critical interactions, such as those between plants and their pollinators, which can have lasting effects monetarily and ecologically (Kearns et al., 1998; Burkle et al., 2013).

The benefits of species diversity

There are numerous positive ecological benefits associated with species diversity, including increased resource use efficiency, improved carbon fixing, and increased decomposer activity (Balvanera et al., 2006; Cardinale et al., 2006; Ptacnik et al., 2008). In addition, communities with diverse species assemblages tend to be more resilient to disturbances, such as introduced species, or the loss of individual species from the community. Increased species diversity has also been found to increase the functional diversity of the system, that is, with more species come more traits that can influence ecosystem properties (Tilman et al., 2001). Increased species diversity can also create redundancy, where multiple species provide the same ecosystem service (Rosenfeld, 2002). This redundancy can act as a hedge against adverse events, such as a droughts, where a more diverse community is less likely to collapse in extreme conditions than a less diverse community (Rosenfeld, 2002). The classification of species as redundant or not is highly dependent on the ecosystem function under consideration, such that species which are redundant with regard to one function may not make redundant contributions to another. As a result, determining the contributions of individual species to the overall function of an ecosystem is often difficult.

While the functional contributions of most species in an ecosystem are difficult to define, there are some species that exert a large amount of influence on their communities relative to their biomass (Mouquet et al., 2012). These highly interactive species are known as keystone species and include: wolves, sea otters, and sea stars (Paine, 1966; Bond, 1994; Soulé et al., 2005). The interactions of these keystone species with the rest of the species in their community drives the community towards a stable state (Libralato et al.,

2006) that encourages more diversity. Their removal from a community, on the other hand, often results in a decrease in the local diversity (Ebenman and Jonsson, 2005), for example, the removal of sea otters from a kelp forest eventually leads to a system dominated by sea urchins which decimate the kelp forest and create what are known as urchin barrens (Bond, 1994). Keystone species certainly shape their ecosystems, they do not, however, exist in isolation. The importance of keystone species lies in how they interact with other species (Shurin and Allen, 2001; Mouquet et al., 2012). However, we still don't fully understand how the other species contribute to community structure and function (Lewinsohn and Cagnolo, 2012).

Ecological communities as interaction networks

While we may not know the role of each individual species, it is widely believed that the distribution of interactions in a community is directly related to the persistence and function of that community (May, 1972; Pimm et al., 1991; McCann, 2000). Interactions between species tend to follow certain patterns based on the level specialization of the species involved. Pollinators, for example, tend to have very restricted or specialized diets, meaning most species tend to interact with a small fraction of the plants in the community (Ings et al., 2009). In contrast, there are many freshwater species that have very general diets, and as a result interact with a variety of different species (Woodward and Hildrew, 2002). In some cases it has been observed that specialist species interact with subsets of the species that generalists interact with, leading to a nested interaction structure (Bascompte et al., 2003). In other cases, interactions are divided amongst groups (or modules) of species such that species in one module interact more with each other than with species in other modules (Fortuna et al., 2010). The presence of these and other structures, and the contributions of each species to the structure of the community, are most easily detected using a network approach.

In a network context, species are represented as network nodes, with interactions (e.g., pollination or predation) forming the links between nodes (Fig. 1). Conveniently, these networks can be represented as a matrix with rows representing consumers (butterflies) or predators and columns representing resources or prey (plants; Fig. 1). For example, in Fig. 1, the red butterfly interacts only with the blue flower, in this case we would assign a 1 to the matrix cell at the intersection

of the row representing the red butterfly *4* and the column representing the blue flower *1*.

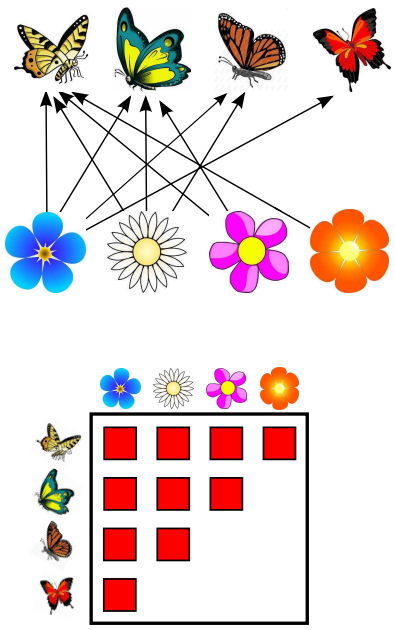


Figure 1: An example plant-pollinator network shown as an interaction network (top) and as an interaction matrix (bottom). This example network shows a perfectly nested interaction structure, with some species interacting with subsets of the species that others interact with.

Organization of ecological networks

Organizing communities (such as the pollination community described in Fig. 1) as ecological networks, allows for the analysis of not only the community but also the way in which individual species come together to form that community. How these interactions are organized can contribute to our understanding of community function, and help us to identify the contributions of a particular species to that function. For example, in pollination networks the interactions between species tend to be nested, where specialist species tend to interact with subsets of the species that the more generalist species interact with (Bascompte et al., 2003). While the pattern of nested interactions has previously been related to the stability of ecological networks (Thébault and Fontaine, 2010), recent work suggests that nestedness alone may not as strong a contributor to stability as previously thought (Strona and Veech, 2015). However, nestedness is thought to be an important structural component of the community (Thébault and Fontaine, 2010). The butterfly pollination network in Fig 1 is an example of a nested network. Antagonistic networks (e.g., predator-prey or host-parasitoid), in contrast, tend to show a more modular structure. A modular structure is where the interac-

tions are divided into their own groups or modules such that species in a particular module tend to interact more with each other and than with species from other modules (Thébault and Fontaine, 2010). The host-parasitoid network in Fig. 3 is an example of a modular network, where we have two distinct groups of species interacting.

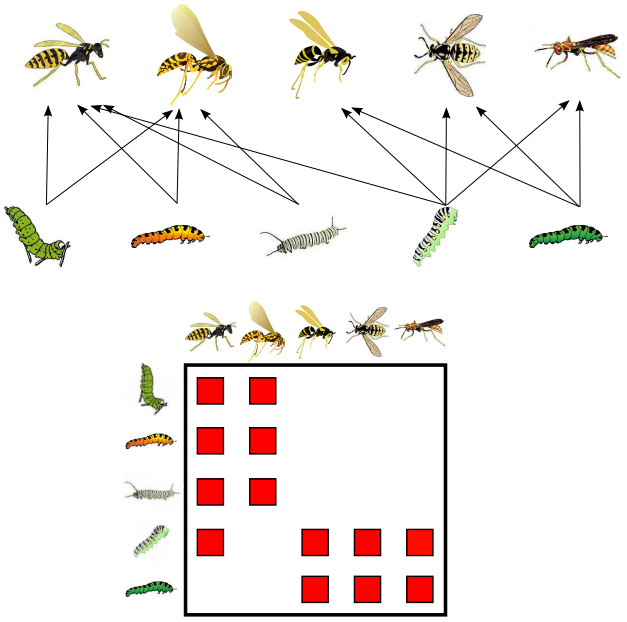


Figure 2: An example host-parasitoid network shown as an interaction network (top) and as an interaction matrix (bottom). This example network shows a modular interaction structure, where we have two modules. In this example, most species interact only with species from their same module except for a single host species which acts as a hub between the two separate modules.

Ecological networks are also able to provide insight on the importance or vulnerability of individual species. For example, Saavedra et al. (2011) found that the species that contributed most to the nested structure of a network were also the most prone to extinction. Another study by Rodriguez-Cabal et al. (2013) found that a reduction in the population of a critically-important species resulted in the complete disassembly of a community network. There have also been studies looking at the contribution that small groups of species make to network structure. For example, a primary producer, a secondary consumer, and a primary predator form a tri-trophic chain. An increase in the number of these trophic chains in a community network has been shown to correlate with an increase in network stability (Stouffer and Bascompte, 2010). Expanding on the organization of species into small functional groups is the concept of network motifs (Milo et al., 2002; Stouffer et al., 2007). Network motifs provide meso-scale approach (i.e., an approach somewhere between the individual species and the full network) to characterizing large ecological networks, by breaking them down into small groups that can be thought of as the building blocks of the larger network. Furthermore, recent studies have expanded on the network motif concept to

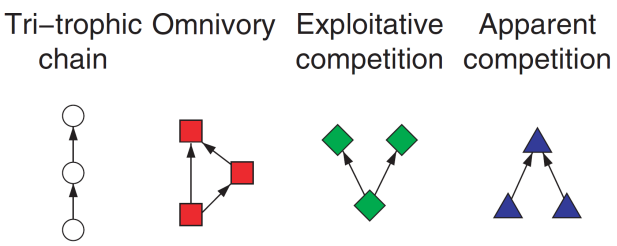


Figure 3: The arrangement of three species into different sets of motifs that correspond to ecologically relevant species interactions: tri-trophic chain, omnivory, exploitative competition, and apparent competition. The presence of these motifs in food-webs has been shown to have a stabilizing effect, buffering the community from disturbances (Stouffer and Bascompte, 2010).

quantify the interaction profile, or network role, of individual species based on their position within the various motif structures that make up the network (Stouffer et al., 2012; Baker et al., 2015). Thus, we not only have a way to characterize the network based on how small groups of species interact, we also have a way to characterize the way in which individual species contribute to the overall network structure.

Aims and hypotheses

The aim of this thesis is to explore the variation of ecological network structure via a network motif perspective. Network motifs allow us to incorporate information about individual species and provide a more detailed view of ecological network structure. To do this, we have broken the thesis into two sections. The first concerns the variability of species' roles in an empirical system, while the second investigates the relationship between motif variation and whole-network measures of variation in simulated networks.

In a recent study, Lewinsohn and Cagnolo (2012) suggested that the results from Stouffer et al. (2012) were intriguing for predicting community persistence from taxonomic profiles alone. However, Lewinsohn and Cagnolo brought into question the viability of using network motifs and species' roles by referencing a study by Kaartinen and Roslin (2011) that showed that species composition was quite variable while network attributes were far more resilient. The first chapter seeks to answer this question posed by Lewinsohn and Cagnolo (2012) by using the very same networks that were used by Kaartinen and Roslin (2011) to determine if species' roles show the same level of consistency that they did in Stouffer et al. (2012). I also hypothesized that if variation in species' roles over space and time was observed, this variation might be re-

lated to fundamental properties of the system such as the isolation of samples sites due to habitat fragmentation.

The second section of the thesis investigated the variability of network structure. I hypothesized that for a given level of connectance, nestedness, or modularity, there exists a large amount of potential variation in network structure that is otherwise obscured by these whole-network measures. Classification of ecological networks based on their nestedness or modularity is a common practice but, by classifying networks in this way, we may overlook important structural differences. Our approach uses network motifs and species participation in those motifs to classify simulated networks across three scales, whole-network, sub-network (network motifs), and the individual species level (species participation in motif structures). I argue that motif-scale and participation-scale network structure will show more variation than the macro-scale measures of network structure. In addition, I argue that for a given number of interactions in the community motif- and participation-scale network structures allow for a more meaningful description of the structure of a network than the standard macro-scale measures.

Together, these studies investigate how variation at different scales can contribute to our understanding of ecological networks. Our results have implications for how we classify networks and provide a deeper understanding of how individual species contribute to the overall network structure.

Species' roles in food webs show fidelity across a highly variable oak forest

Abstract

Ecological communities are composed of many species and an intricate network of interactions between them. Because of their overall complexity, an intriguing approach to understanding network structure is by breaking it down into the structural roles of its constituent species. The structural role of a species can be directly measured based on how it appears in the network motifs–the basic building blocks of complex networks. Here, we study the distribution of species' roles at three distinct spatio-temporal scales (i.e., species, network, and temporal) in host-parasitoid networks collected across 22 sites over two years within a fragmented landscape of oaks in southern Finland. We found that species' roles for hosts and parasitoids were heterogeneously distributed across the study system but that roles are strongly conserved over spatial scales. In addition, we found that species' roles were remarkably consistent between years even in the presence of disturbances (e.g., species turnover). Overall, our results suggest that species' roles are an intrinsic property of species that may be predictable over spatial and temporal scales.

"*Species' roles in food webs show fidelity across a highly variable oak forest*"
Nick J. Baker, Riikka Kaartinen, Tomas Roslin, Daniel B. Stouffer
Ecography, Volume 38, Issue 2, Pages 130–139, February 2015.

Introduction

Global biodiversity is being threatened by a variety of anthropogenic drivers (Sala et al., 2000), and the biodiversity loss that can result from these drivers may in turn lead to the loss of beneficial ecosystem functions, such as pollination and decomposition (Dobson et al., 2006). Notably, the loss of just a single species can reverberate through a community, impacting the abundances of other species and the susceptibility of the community to further disturbance (Ives and Cardinale, 2004). It has been shown, for example, that changes in herbivore abundances can induce trophic cascades that directly alter plant and predator abundances (Lewis, 2009).

There are many potential drivers of biodiversity loss, including non-native species, climate change, and habitat loss and destruction (Sala et al., 2000) and these drivers can disrupt ecological communities in a variety of ways. For example, the introduction of non-native species can extirpate native species by out-competing or preying on them and can induce changes in local habitats (McGeoch et al., 2010). Similarly, shifts in the local climate can alter community composition (Koh et al., 2004) and have been shown to disrupt interactions between species (Gilman et al., 2010; Harley, 2011). The loss or destruction of local habitat can lead to increased isolation, decreasing dispersal efficiency (van der Putten et al., 2004), and changes to the competitive balance between organisms (Kareiva, 1987), all of which which can have additional community-level consequences via changes in species-species interactions.

One holistic approach to understanding how disturbances influence species is to determine their impact on a community's network of interactions (Ings et al., 2009). This approach allows us to assess changes to interactions within a community, without making *a priori* decisions about the relative importance of any particular interaction (Tylianakis et al., 2008). Unfortunately, analyses at the network level are often challenging due to the inherent complexity of these systems (Memmott, 2009). One way in particular that researchers have attempted to gain insight into ecological networks, despite their complexity, is through the concept of network motifs (Milo et al., 2002, 2004). Network motifs provide a way to simplify the characterization of large networks by breaking them down into meso-scale subnetworks made up of a limited number of species (Bascompte et al., 2005; Camacho et al., 2007; Stouffer et al., 2007). The underlying principle is that any network can be decomposed into a unique set of mo-

tifs that act as the building blocks of the larger network and which, when reassembled, would form the original network (Milo et al., 2002). These smaller subnetworks can also represent sets of ecological interactions that are widely regarded as important, such as apparent and exploitative competition (Holt, 1997).

In addition, this concept of motifs has been expanded to quantify the roles of individual species within a network (Stouffer et al., 2012). Just as motifs are the meso-scale building blocks of networks (Bascompte and Stouffer, 2009), species' roles offer a species-centric perspective of network structure by describing the configuration of a species' interactions in the network. Moreover, rather than having a single measure with which to quantify overall network structure, we can decompose a network into the complete distribution of roles of each of its constituent species, providing an enticing alternative to community- or network-level analyses.

We follow this species-centric approach here to study changes in species' roles through space and time within a fragmented host-parasitoid community. A previous study has demonstrated that this system is characterized by considerable spatial and temporal variability in species composition and diversity (Kaartinen and Roslin, 2011). Moreover, the variation observed in species composition seems largely unpredictable. Paradoxically, the host-parasitoid network structure overall remained relatively consistent between years and across the landscape (Kaartinen and Roslin, 2011, 2012). While the overall structure of the host-parasitoid networks remained consistent through space and time, previous research indicates that the changes in species composition and in immigration caused by the fragmentation could alter the interactions in such a way to still create an impact on species' roles (Vázquez et al., 2005).

In order to better understand the potential mechanisms underlying the interplay between species composition, species' roles, and the emergent property of whole-network structure, we systematically investigate the degree to which different predictors influence the distribution of species' roles between species, across space, and over time. Specifically, we first tested whether species' roles are an intrinsic species property, predicted by species identity, independent of the network in which they appear. Second, we analyzed variation in species' roles across a landscape by investigating whether the role of a species depends on the network in which it is found. Third, we explored whether species' roles are consistent over time despite the highly variable nature of our study system.

We then quantified whether and how potential drivers of role variation influenced species' roles and a community's role structure at each level of the analysis. These drivers were all selected because they represent intuitive biological factors that would be expected to contribute to natural variation in species' roles. At the species level, we hypothesized that feeding guild, abundance, number of interactions, or degree of specialization would explain variation in species' roles. At the network level, we hypothesized that related network-scale metrics would explain variation in species' roles across the landscape; these included proportion of species belonging to a particular feeding guild, species richness of the network, network connectance, and network specialization. Lastly, at the temporal level, we hypothesized that habitat fragmentation, changes in species composition between years, and interaction turnover would explain variation in species' roles through time.

Methods

Empirical data

The interaction networks studied here come from a fragmented range of European oaks (*Quercus robur*) in southern Finland with oaks scattered as large stands, small stands, and as isolated trees. As habitat islands, these oak trees sustain a high diversity of Hymenopteran and Lepidopteran species and their associated parasitoids (Kaartinen and Roslin, 2011). The host-parasitoid communities were sampled from 22 individual oak trees (henceforth referred to as sites) spread over an area of approximately $5km^2$. They were sampled across two years (2006 and 2007), giving a total of 44 host-parasitoid networks (i.e., each site-year combination has a corresponding network). Across all networks, there were 28 leaf-miner and galler host species and 60 leaf-miner and galler parasitoid species (Supplementary material Appendix 1, Fig. A1 and A2). Interactions between species were documented following successful emergence of a parasitoid from a host species (Kaartinen and Roslin, 2011).

Here we consider all events that indicate the existence of a host-parasitoid interaction as qualitative (binary), and therefore independent of the empirically-observed interaction strength. Reduction of quantitative networks to their qualitative equivalent may result in

rare species or interactions contributing more than they otherwise would to any subsequent characterizations (Banašek-Richter et al., 2004). To determine if our results were indeed influenced by rare species or interactions, we compared the results for the qualitative networks to those expected if we had resampled the quantitative networks proportional to the observed interaction frequencies (Supplementary material Appendix 2). Overall, the resampling analysis indicated that none of our primary results were influenced by our use of qualitative networks.

Network motifs

Previous work in multitrophic food webs has focused primarily on three-species motifs within ecological networks (Bascompte et al., 2005; Camacho et al., 2007; Stouffer et al., 2007, 2012). Unfortunately, there are only two possible three-species motifs in bipartite networks (Fig. 4) in contrast to the 13 possible in multitrophic networks (Stouffer et al., 2007). This distinction is driven by the fact that bipartite networks are two-mode networks made up of two distinct groups of species that may only interact between but not within groups. Therefore, to robustly explore species' roles in bipartite networks, we have expanded the previous methodology to include all of the bipartite motifs from two to six species, giving a total of 44 motifs (Supplementary material Appendix 3, Fig. A27). Though it reduced the meso-scale complexity, our results were consistent when only considering motifs up to size four or five.

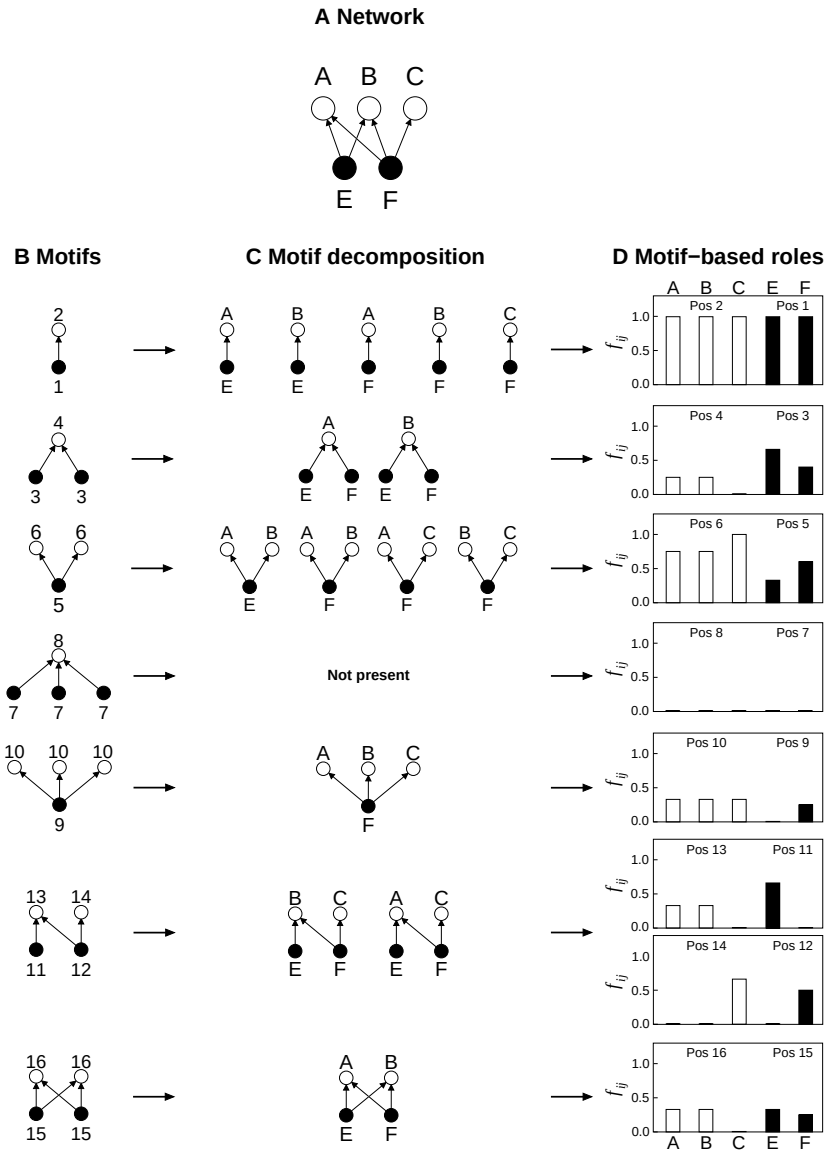


Figure 4: Quantifying species' roles from a hypothetical host-parasitoid food web **A,** The food web contains three parasitoid species (A, B, and C) and two host species (E and F). **B,** In bipartite networks, there are one unique two-species motif, two unique three-species motifs, and four unique four-species motifs, with two, four, and ten unique positions respectively. **C,** The food web can be decomposed into all species combinations whose interactions match the motif's configuration. Note that not all motifs must be observed. **D,** The role of a species is defined as the relative frequency with which it appears across the structurally-unique positions in the different motifs. Importantly, the relative frequencies are normalized within each motif size class. Note that, some positions are not unique and can be occupied by multiple species simultaneously (e.g., position 3 is occupied by two host species).

Species' roles in bipartite networks

To measure the roles of all species in a network, we first calculated the frequency of each of the 44 bipartite motifs that appear in each bipartite network (Fig. 4). Though each motif of size s is, by definition, composed of s species, each species does not always appear in a unique position within that motif for reasons of symmetry (Kashtan et al., 2004; Milenković and Pržulj, 2008; Stouffer et al., 2012). For example, in the two species motif A→B, the positions of A and B are uniquely defined by the direction of the interaction

between them. Across the 44 bipartite motifs used in this study, there are a total of 148 unique positions (Supplementary material Appendix 3).

To quantify the role of species i in network n based on the observed motif frequencies, we enumerated the frequency $c_{ij|n}$ with which species i appears in each unique motif position j in network n. For all species i, this enumeration process creates a vector

$$\overrightarrow{c}_{i|n} = \{c_{i1}, c_{i2}, \ldots, c_{i148}\}_n \,, \tag{1}$$

which is a multidimensional measure of how that species' interactions are arranged in its community's network: its role. Because some species have more interactions, they will naturally appear in more motifs than other species; as a result, some species will tend to have larger values of $c_{ij|n}$. To control for this effect, we normalize the vector $\overrightarrow{c}_{i|n}$ within each motif size class s (i.e., two, three, four, five, and six species). Each species in a network is then described by its normalized role $\overrightarrow{f}_{i|n}$ where all $f_{ij|n}$ are given by

$$f_{ij|n} = \frac{c_{ij|n}}{\sum_k c_{ik|n}\delta_{jk|s}} \,, \tag{2}$$

where the sum is across all motif positions and $\delta_{jk|s}$ is Kronecker's delta ($\delta_{jk|s} = 1$ if positions j and k are in the same group s and $\delta_{jk|s} = 0$ otherwise; in this case the group is motif size class). The role, $\overrightarrow{f}_{i|n}$ of a species, therefore, describes its relative tendency to appear across the different motif positions throughout the network. More generally, we can consider the roles defined here as a quantitative representation of a species' "interaction niche" since it describes how its host-parasitoid interactions are embedded within the larger space of the network (Fig. 4).

Fidelity of species' roles

Here, we aim to determine whether consistency of roles is maintained in the presence of disturbances. In order to first quantify consistency of roles, we introduce the concept of "role fidelity" which can be thought of as the degree of predictability in the distribution of species' roles at a given scale of the data. Here, we specifically examined the strength of fidelity at the species, network, and temporal levels. The roles of host and parasitoid species were analyzed separately since they always represent orthogonal sets to each other (Fig. 4). This separation prevents the permutational analysis from

assigning a role of a parasitoid to that of a host and vice versa. From this perspective, species fidelity would indicate that species' roles were significantly associated with species' identity across both sites and years. Similarly, network fidelity would indicate that the subset of roles observed in a network are a significantly non-random subset of all possible roles, and temporal fidelity would indicate that the subset of roles observed at a site in 2006 were not significantly different from those observed at that same site in 2007.

Our approach here is based on between- and within-group comparisons of role fidelity in a fashion analogous to a traditional analysis of variance. We note, however, that there are multiple ways in which fidelity could emerge and which could provide fruitful avenues for future study. One such way is via differences in species abundances, where it might be reasonable to expect more abundant species to show more consistent role fidelity than rare species. Though we have worked to control for the influence of rare species via the resampling analysis presented here, this does not eliminate the possibility that underlying mechanics driving species abundance may also drive aspects of any observed role fidelity.

Species fidelity

We first tested whether or not species identity explained a significant amount of the total variation present in the observed species' roles. This is analogous to determining if there is significant clustering of species' roles on the basis of species identity. One approach to do this is to use permutational multivariate analysis of variance (PERMANOVA); the methods of a PERMANOVA are an extension of the traditional analysis of variance that generates a multivariate analogue to Fisher's F-ratio based on total dissimilarity relative to within-group dissimilarity (Anderson, 2001). Note that, our method is not the same as a traditional PERMANOVA, due to there being no true replication within this study. Instead, we are using the PERMANOVA as a way to test for the clustering of data at various levels of community organization via a permutational approach.

Within our PERMANOVA, the total dissimilarity D across all species and networks is given by

$$D = \frac{1}{N} \sum_{i=1}^{N-1} \sum_{j=i+1}^{N} b_{ij}^2 , \tag{3}$$

where N is the total number of species' roles and b_{ij} is distance between role i and role j (we will describe the choice of a distance metric later). This measure of total dissimilarity treats roles as independent from networks. As a result, comparisons between species' roles are made within and between networks in the course of the analysis. For any group k, the within-group dissimilarity d_k is given by

$$d_k = \frac{1}{g_k} \sum_{i=1}^{N-1} \sum_{j=i+1}^{N} b_{ij}^2 \delta_{ij|k}\,, \tag{4}$$

where g_k is the number of roles in the group and $\delta_{ij|k}$ is Kronecker's delta (as before, $\delta_{ij|k} = 1$ if role i and role j are roles in the same group k and $\delta_{ij|k} = 0$ otherwise). Note that the grouping or clustering here can be done at a variety of levels. For example, grouping by species identity would give within-group dissimilarity d_k for all roles played by species k across the whole data set. Likewise, grouping by network would give within-group dissimilarity d_k for all roles played by species in network k. Total within-group dissimilarity across all species and networks is then given by $D_w = \sum_k d_k$, and the total dissimilarity and within-group dissimilarity are finally combined to give the test statistic $F = \frac{(D-D_w)/(g_k-1)}{D_w/(N-g_k)}$ (Anderson, 2001).

To test significance of any level of clustering, one can create a null distribution of the test statistic F by directly permuting the observed data (Anderson, 2001). Specifically, we randomly shuffle the labels on the roles and recalculate F^*. After repeating this process to create a large ensemble of test statistics, the p-value is given by the proportion of random test statistics that are as or more extreme than the observed test statistic (Veech, 2012).

A key step for using PERMANOVA is identifying an appropriate distance metric dependent on the data being analyzed. Recall that species' roles specify a set of relative frequencies with which a species appears across different motif positions. We therefore chose the Bray-Curtis distance which is a robust measure of dissimilarity for multiple properties of ecological communities (Faith et al., 1987; Anderson, 2001; Anderson and Robinson, 2003).

To quantify overall species fidelity with a PERMANOVA, we followed the procedure outlined above with all roles $\overrightarrow{f}_{i|n}$ as the dependent variable and species identity as the grouping factor. We also restricted the randomizations for generation of the null distribution to the level of individual networks (i.e., a site-year combination) such that species identities were shuffled only within the network that

they appear in (Anderson, 2001) to account for non independence of species' roles within each network. We conducted the analysis using the adonis function from the *vegan* package (Oksanen et al., 2012) in R 2.15.1 (R Core Team, 2013), and we generated 4999 permuted values for the null distribution. Species that appeared in just one network were excluded from this analysis as we could not calculate their within-group distances.

In order to isolate species which contribute more or less to the overall variation of species' roles, we also calculated the fidelity of roles at the individual species level. Specifically, we use Eq. (4) to calculate the overall dissimilarity d_k of all empirically-observed roles for each species k. Here, we again conducted a permutation test where we randomized the species' identities within networks and calculated the test statistic d_k^*, and we repeated this process 4999 times to generate a null distribution of test statistics. We then used a direct test to compute $p_k = P(d_k^* \leq d_k)$, the proportion of randomizations that showed equivalent or greater similarity than that observed empirically (Veech, 2012). When $p_k < 0.05$ (at $\alpha = 0.05$), there is significant species fidelity since the observed subset of roles for species k represent a tightly-clustered, non-random subset of all possible roles.

Network fidelity

To calculate network fidelity, we followed a similar procedure to that of the species-fidelity calculations. First, we ran a PERMANOVA to determine if network identity (i.e., site-year combinations), explained a significant amount of the total variation present in the species' roles; the roles $\overrightarrow{f}_{i|n}$ were once again the dependent variable with network identity as the grouping factor and unrestricted permutations.

We then decomposed the PERMANOVA results to the individual network level following Eq. (4), except that the grouping index k now indicates the network identity and Kronecker's delta $\delta_{ij|k} = 1$ when the roles i and j are both from network k and $\delta_{ij|k} = 0$ otherwise. As before, when $p_k < 0.05$ (at $\alpha = 0.05$), there is significant network fidelity since, across sites and years, the subset of roles observed in network k are a tightly-clustered, non-random subset of all possible roles.

Temporal fidelity

To quantify temporal fidelity, we first ran a PERMANOVA analysis with the roles $\overrightarrow{f}_{i|n}$ as the dependent variable and site identity and an interaction between site identity and year as the grouping factors. Year was not included as a separate grouping factor because we were only interested in the variation of roles at a site between years and not differences between years independent of site. To control for underlying variation across sites, we restricted the randomizations in this PERMANOVA to be within the same site. Note that, in contrast to species or network fidelity, we are interested here in the *similarity* of species' roles between sample years at each site when referring to temporal fidelity. Within our statistical framework, an indication of temporal fidelity is provided by a non-significant interaction between site identity and year in the PERMANOVA since such an interaction would imply that species' roles tended to differ between years at the different sites. Next, we obtained results at the individual site level by running analogous PERMANOVA analyses on a site-by-site basis following Eq. (4). The grouping index k now indicates the site identity and Kronecker's delta $\delta_{ij|k} = 1$ when the roles i and j are both from site k and $\delta_{ij|k} = 0$ otherwise.As before, when $p_k \geq 0.05$ (at $\alpha = 0.05$), there is temporal fidelity at site k since the subset of roles observed in 2006 were *not* statistically distinguishable from the subset of roles observed in 2007.

Potential drivers of species and network fidelity

In addition to quantifying levels of fidelity in our empirical networks, we also aimed to identify potential drivers of differences in fidelity across species and networks. At the species level, we hypothesized that species' feeding guild, abundance, number of interactions, or degree of specialization could help explain why some species showed fidelity as opposed to others. Abundance was measured as the rank abundance for each species in their network (the least abundant species was given the lowest rank), number of interactions was given by the ranked number of interactions for each species in the qualitative network (the species with the fewest interactions was given the lowest rank), and specialization was calculated using the dfun function in the *bipartite* package (Dormann et al., 2008) in R 2.15.1 (R Core Team, 2013). We performed a χ^2 test to determine if the proportion of species belonging to a particular feeding guild was related to observed species fidelity. In addition, we quantified the

relationship between each of the other drivers and and whether or not the species showed significant fidelity with a generalized linear mixed model with species identity as the random effect (to control for additional variation between species), binomial errors, and logit link function using the *lme4* package (Bates et al., 2013) in R 2.15.1 (R Core Team, 2013). We simplified this full multivariate model by removing predictors until no significant reduction in AIC occurred (Crawley, 2007).

We also explored the effect of the corresponding metrics at the network level (i.e., each network in the data set), where we tested the influence of the proportion of host species that belonged to the leaf-miner feeding guild, the proportion of parasitoid species that belonged to the leaf-miner parasitoid feeding guild, species richness, connectance, and specialization on network fidelity. Species richness was equal to the total number of host and parasitoid species in a given network, connectance was given by $L/(H * P)$, where L is the number of links, H is the number of host species and P is the number of parasitoid species. Specialization was calculated using the H2fun function in the *bipartite* package (Dormann et al., 2008) in R 2.15.1 (R Core Team, 2013). We quantified the relationship between each driver and and whether or not the network showed significant fidelity with a generalized linear model, binomial errors, and a logit link function using the *glm* function in R 2.15.1 (R Core Team, 2013). We simplified this full multivariate model by removing predictors until no significant reduction in AIC occurred (Crawley, 2007).

Potential drivers of temporal fidelity

We also aimed to identify potential drivers of differences in fidelity through time. Recall that the empirical data studied here was collected in a heavily fragmented ecosystem and there was considerable species turnover between years at each site (Kaartinen and Roslin, 2011). Changes in the composition of species, as a result of natural turnover or from reduced immigration pathways due to habitat fragmentation, could also potentially alter how species interact across the sites (Laliberté and Tylianakis, 2010; Tylianakis et al., 2008; Kaartinen and Roslin, 2011). We therefore hypothesized that changes in any of fragmentation, species composition, or changes in interactions observed at a site would lead to increased variability in species' roles, thereby decreasing the fidelity of species' roles between years.

To quantify changes in species composition with time, we calculated the species turnover of the host and parasitoid communities at each site between 2006 and 2007 using the Whittaker index (Whittaker, 1960) since it is a robust measure of beta diversity (Koleff et al., 2003); a value of zero indicates a community with no species turnover between years while a value of one indicates a community with complete species turnover. To quantify changes in species' interactions with time, we calculated interaction turnover (β_{WN}) at each site by measuring pairwise differences in the interactions observed between years (Poisot et al., 2012). Just like species turnover, a value of zero indicates a community with identical interactions between years while a value of one indicates a community with completely different interactions. Finally, we quantified the expected influence of habitat fragmentation via a modified measure of connectivity that describes expected insect immigration at each tree (Kaartinen and Roslin, 2011). The values of habitat connectivity are rescaled here such that zero indicates a poorly-connected, highly-isolated site while the value of one indicates a site that is not isolated.

To assess whether species turnover, interaction turnover, and habitat connectivity act as drivers for increased or decreased temporal fidelity of host or parasitoid roles, we quantified the relationship between each measure and the measure of temporal fidelity for each site with a generalized linear model, binomial errors, and a logit link function using the *glm* function in R 2.15.1 (R Core Team, 2013). We simplified this full multivariate model by removing predictors until no significant reduction in AIC occurred (Crawley, 2007).

Results

Species-level fidelity

Species type	Source of variation	d.f.	S.S.	M.S.	F	R^2	p
Hosts							
	Species identity	21	10.019	0.477	4.098	0.216	< 0.001
	Residuals	313	36.446	0.116		0.784	
Parasitoids							
	Species identity	48	15.679	0.327	3.371	0.249	< 0.001
	Residuals	487	47.188	0.097		0.751	

Table 1: Summary of results from the species-level PERMANOVAs for host and parasitoid species. Permutations in the PERMANOVAs were restricted to only shuffle roles within each network to account for non independence of species' roles within an interaction network.

The species-level PERMANOVA analysis indicate that species identity explained a significant amount of role variability of both hosts and parasitoids ($F_{21,313}$, $p < 0.001$ and $F_{48,487}$, $p < 0.001$, respectively; Table 1). When examining the way that individual species contributed to overall species fidelity, we observed that significantly more host and parasitoid species showed role fidelity than would be expected at random (8 out of 21 host species, $p < 0.001$; 16 out of 49 parasitoid species, $p < 0.001$). Overall, these analyses suggest that species identity is a significant predictor of the role of a given species in the network and that the roles of individual species tend to be conserved across the different sites and between the two years.

Drivers of species fidelity

We found that none of feeding guild, abundance, number of interactions, or degree of specialization were significantly related to the species fidelity of host or parasitoid roles.

Network fidelity

Species type	Source of variation	d.f.	S.S.	M.S.	F	R^2	p
Hosts							
	Network	43	8.880	0.207	1.599	0.191	< 0.001
	Residuals	291	37.586	0.129		0.809	
Parasitoids							
	Network	43	13.795	0.321	3.217	0.219	< 0.001
	Residuals	492	49.072	0.099		0.781	

Table 2: Summary of results from the network-level PERMANOVAs for host and parasitoid species. Permutations in each PERMANOVA were unrestricted.

Results from the network-level PERMANOVA analysis indicate network identity explained a significant amount of role variability for both hosts and parasitoids ($F_{43,291}$, $p < 0.001$ and $F_{43,492}$, $p < 0.001$,respectively; Table 2).

When examining the way that individual networks contribute to network fidelity, we found that significantly more networks showed fidelity of host and parasitoid roles than would be expected at random (9 out of 44 networks, $p < 0.001$; 15 out of 44 networks, $p < 0.001$, respectively). Overall, these analyses suggest that the roles within the different networks are significantly more similar to each other than they are to roles from other networks.

Drivers of network fidelity

We found that proportion of species belonging to a particular feeding guild, species richness, and connectance were not significantly related to the network fidelity of host or parasitoid roles (all removed from model). The specialization of the network was significantly related to the network fidelity of host roles ($z_{43} = -2.088$, $p = 0.037$) but not of parasitoid roles (removed from model; Fig. 5).

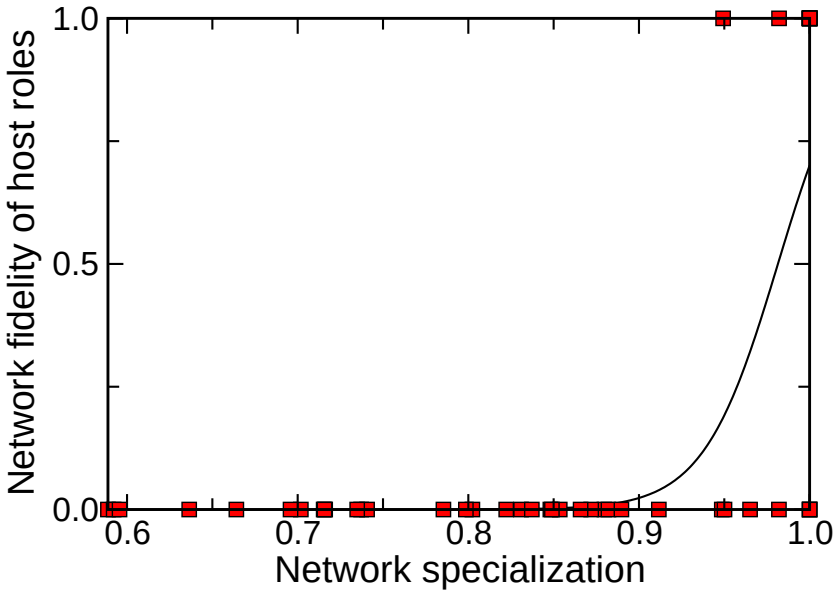


Figure 5: The relationship between network fidelity of host roles and the specialization of each network. We observed a significant relationship between the magnitude of network fidelity of host roles and host specialization with more specialized networks showing greater fidelity of host roles ($p = 0.037$).

Temporal fidelity

Species type	Source of variation	d.f.	S.S.	M.S.	F	R^2	p
Hosts							
	Site	21	5.317	0.253	1.975	0.113	0.026
	Site:Year	22	3.817	0.173	1.353	0.081	0.026
	Residuals	297	38.078	0.128		0.806	
Parasitoids							
	Site	21	7.928	0.378	3.793	0.124	< 0.001
	Site:Year	22	5.993	0.272	2.737	0.094	< 0.001
	Residuals	504	50.168	0.099		0.782	

Table 3: Summary of results from the temporal-level PERMANOVAs for host and parasitoid species. Permutations in the PERMANOVAs were restricted to only shuffle roles within each site (i.e., between years) to assess differences in the clustering of roles in 2006 and 2007.

For host and parasitoid species, our temporal PERMANOVA analysis indicates that site identity and a site-by-year interaction both explained a significant amount of role variability ($F_{21,297}$, $p = 0.026$,$F_{22,297}$, $p = 0.026$, and $F_{21,504}$, $p < 0.001$, $F_{22,504}$,

$p < 0.001$, respectively; Table 3). This suggests that the roles in at least some of the sites were variable for both host and parasitoid species. When breaking down these results by site, we found that host roles were significantly different between years at only 3 out of 22 sites ($p = 0.095$) while parasitoid roles were significantly different between years at 9 out of 22 sites ($p < 0.001$).

Drivers of temporal fidelity

Of the hypothesized drivers of role variability at the temporal level, none of habitat fragmentation, parasitoid species turnover, or interaction turnover, were significantly related to the temporal fidelity of host or parasitoid roles (all removed from the model). Host species turnover, however, was significantly related to the temporal fidelity of parasitoid roles ($z_{21} = 1.991$, $p = 0.047$; Fig. 6).

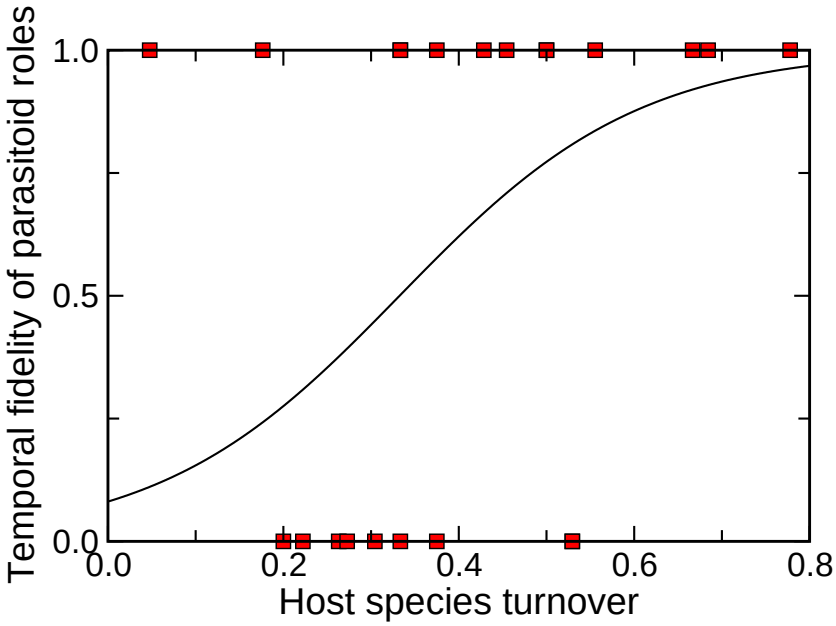


Figure 6: The relationship between temporal fidelity of parasitoid roles and host species turnover. We found that the temporal fidelity of parasitoid roles was significantly related to host turnover such that increased turnover was positively related to increased fidelity ($p = 0.047$).

Discussion

Overall, we found that the roles for host and parasitoid species showed signs of fidelity at the level of species and networks, and at the level of sites examined through time. Of the hypothetical drivers of role fidelity, we first found a significant relationship between network specialization and network fidelity of host roles such that net-

works that showed fidelity were significantly more specialized than those that did not. This may suggest that there is less niche overlap in these networks (Poisot et al., 2013) resulting in increased role overlap, and that turnover in these networks is more predictable because there are fewer interaction niches that can be filled. In addition, we found that the temporal fidelity of parasitoid roles was significantly related to host turnover such that increased turnover was positively related to increased fidelity. This result is particularly counter intuitive since we would have expected that lower host species turnover between years would act as a stabilizing factor for parasitoid roles. What's more, high host turnover was correlated with high parasitoid turnover as well. Lastly, we found that our results are consistent when accounting for the potential influence of rare species in our networks. Beyond predicting the roles themselves, the predictable and unpredictable ways in which these communities vary across space and time imply that there is much to understand about the broader interplay between species, network, and temporal fidelity.

The implications of species fidelity

Despite hypotheses to the contrary (Lewinsohn and Cagnolo, 2012), we found that hosts' and parasitoids' roles are significantly clustered by species identity. This conclusion is in general agreement with a previous study that concluded that phylogenetically-related species showed similar roles, independent of ecosystem type (Stouffer et al., 2012). Our study therefore provides additional evidence that species' roles may be an intrinsic species characteristic. Of potentially greater importance here, however, are the far-reaching implications of species fidelity in a community that experiences substantial turnover (Lewinsohn and Cagnolo, 2012).

Though the roles we study here are quantified at the level of individual species, it is clear that the role of any particular species is a by-product both of that species' interactions and the interactions of the other species in the community (Luczkovich et al., 2003; Stouffer et al., 2012). To better illustrate this fact, consider a hypothetical community composed of two parasitoid species, both of which interact with two host species. If one host species leaves this community, the roles of all three remaining species will necessarily change. In such a situation, the only way in which we could observe significant role fidelity of the remaining species, as we observe here, would be for a new host species to enter the community and take on the *ex-*

act same role that was lost and, what's more, participate in the same interactions.

It would therefore appear that species fidelity imposes multiple constraints on the roles observed within a community and, consequently, food-web structure. In fact, if we know that a specific species is observed in a community, species fidelity allows us to predict both the interaction niche of that same species and, by extension, the interactions of many other species. This interplay between species fidelity and the overall distribution of roles will also help us to better understand the mechanisms underlying the patterns observed at both the network and site levels.

The implications of network fidelity

Our exploration of network fidelity is fundamentally a test of how species' roles are distributed within a landscape context. Our analyses indicated that the roles in any given network were more similar to each other than to the roles found in the other networks. This result suggests that each network is characterized by considerable role "overlap" and likely implies that our individual networks exhibit limited functional diversity (Petchey et al., 2008). A lack of functional diversity might be important particularly since species' interactions have been linked to various measures of ecosystem function, such as community persistence (Stouffer et al., 2012). Alternatively, the combination of low functional diversity and high role overlap seen here indicates the potential of increased redundancy and complementarity which can buffer communities from disturbances (Naeem and Wright, 2003).

Previous research in this system found that, on the basis of whole-network comparisons, the networks themselves maintained their structure across the landscape (Kaartinen and Roslin, 2011). To be fully consistent with our results about network fidelity of species' roles, there must be multiple ways in which distinct species' roles can be combined to produce *equivalent* network structure overall. This may have important implications for studies focusing strictly on whole-network measures as the basis for comparisons over time or through space, as they may be overlooking important meso-scale structural changes.

Comparisons on the basis of species' roles, such as those explored here, can therefore provide a more comprehensive view of ecological networks by disentangling the contributions of individual species to network structure. Since trophic roles and network structure are both thought to relate to overall ecosystem function (Thompson et al., 2012), an open question is whether species-level or network-level predictions are equally informative or whether they provide complementary perspectives (Lewis, 2009).

The implications of temporal fidelity

Though the temporal signal was slightly weaker, we found that the distribution of species' roles across many sites was more consistent between the two years than expected. This result aligns well with previous work that found that the quantitative structure of the food webs in this system changed very little between years (Kaartinen and Roslin, 2012). One of the key differences within our study was that parasitoids' roles showed greater within-site variation between years than did hosts' roles. In contrast to our initial hypotheses, our study allows us to rule out multiple possible explanations for this difference, including interaction turnover and habitat fragmentation. The most parsimonious explanation might then simply be that increased variation of parasitoid roles is attributable to the fundamental ecological asymmetry between the two groups of species: hosts can be observed in a site without parasitoids whereas parasitoids cannot be present without their hosts (Russell, 1989).

Interestingly, we still observed role fidelity even though there was, on average, 50% species turnover and 70% interaction turnover between years. If we return to the hypothetical community that we used when discussing species fidelity, temporal fidelity provides the expectation that nearly all species that depart are replaced by a new species with a comparable role; but at close to a community scale. Given that species' roles are also strongly related to species identity, consistency in network structure should also mean that changes in species composition are imminently predictable. Precisely how to quantify this "predictability" remains an open question for future research since the brief temporal scale of our study does not allow much extrapolation.

Predictable species turnover, in a way that also maintains both the role distribution and network structure of a community, might simply

be a demonstration of the inherent resilience of host-parasitoid communities (Laliberté and Tylianakis, 2010). It might similarly provide an intriguing mechanism with which to maintain ecosystem function when confronted by internal and external disturbances (Walker, 1995). The interplay then between species, network, and temporal fidelity might allow us to make better predictions of overall changes in ecosystem function (Tomimatsu et al., 2013).

Conclusions

Understanding and predicting the importance of individual species to ecological communities is an ongoing challenge in ecological research (Lewinsohn and Cagnolo, 2012). Here, we found that species' roles appear to be an intrinsic species property, that they are broadly conserved across a landscape, and may be conserved over time despite changes in species composition. It will be interesting to determine how easily our results can be extrapolated to other communities, as they might provide a meso-scale platform from which to develop predictions about changes in ecological community structure.

A meso-scale approach to understanding macro-scale measures of ecological networks

Abstract

Analysing ecological communities as complex networks has become an important tool for ecologists. Specific patterns in the organization of species within these networks, such as connectance, nestedness, and modularity have emerged as crucial contributors to the maintenance of biodiversity and community stability. Connectance, the number of links between species in a network, has considerable influence on the overall structure of the network. For example, for given values of connectance and species richness, there exists a network space representing all possible configurations. Within this network space, many networks will have similar measures of nestedness and modularity. These measures provide insight into the general structure of the network, but the level of detail provided is coarse at best. By focusing our attention on these whole-network measures we may be overlooking important variation in the underlying meso-scale network structure. Here we use network motifs, which are sub-networks representing interactions among a small number of species, to quantify the meso-scale structure of ecological networks. Motifs represent patterns of interactions between a small number of species and act as a bridge between the individual species and whole network perspectives. We found that at fixed levels of connectance, nestedness, and modularity the motif profiles of networks and the distribution of species across those profiles showed remarkable dissimilarity. This suggests that networks displaying similar macro-scale structural measures can be composed of vastly different meso-scale structures. Thus, in contrast to previous approaches our meso-scale perspective is tractable and able to capture more detail about the structure of em-

pirical networks and, as a result, provides a clearer lens with which to examine ecological communities.

Introduction

The analysis of ecological communities using a network perspective, where species act as nodes and interactions between species act as links connecting nodes, has become an important tool for ecologists (Ings et al., 2009). The topology of these networks has been shown to contribute to biodiversity maintenance (Bastolla et al., 2009), ecosystem function (Poisot et al., 2013), and the stability of ecological communities (Thébault and Fontaine, 2010; Allesina and Tang, 2012). Early research seeking to understand the effects of network topology on the community, represented by the food web, focused on the density of interactions, or connectance of the network (Dunne et al., 2002; Krause et al., 2003). Over time, focus shifted from the number of interactions to the way in which those interactions were organized. The two main patterns of organization that have received the most focus are nestedness and modularity. A nested pattern is one where specialist species interact with subsets of the species that generalists interact with (Bascompte et al., 2003). A modular pattern is one where groups of species, or modules, tend to have interactions among themselves and few interactions with species from other modules (Olesen et al., 2007).

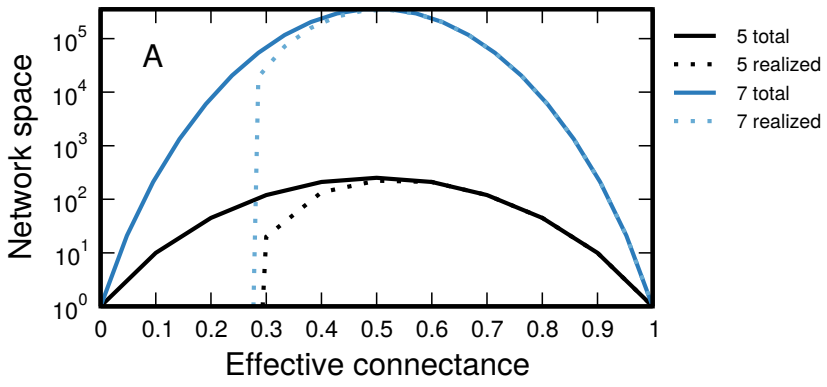


Figure 7: The number of possible undirected networks composed of 5 and 7 species (black and blue lines, respectively) across a range of connectance following Poisot and Gravel (2014). We can further constrain this space by requiring each species in the network to have at least one interaction (dotted lines).

Both nestedness and modularity have been shown to confer positive benefits to ecological communities (Olesen et al., 2007; Bastolla et al., 2009; Thébault and Fontaine, 2010) and are thought to contribute to the overall complexity of these systems (Olesen et al., 2007). Mathematically, these measures are intimately connected with the connectance of the network (Poisot and Gravel, 2014;

Rezende and Stouffer, 2014). Connectance is particularly important as it can impose strict limits on the number of "potential" networks which can be observed for a fixed number of species (Fig. 7). Within this network space, research on empirical networks has argued that nestedness and modularity are antithetical forms of network organization, with nested communities necessarily displaying low modularity and vice versa (Thébault and Fontaine, 2010; Stouffer et al., 2012). Because of this intimate connection it could be argued that connectance, nestedness, and modularity are all sides of the same multi-dimensional coin providing similar macro-scale information about a network.

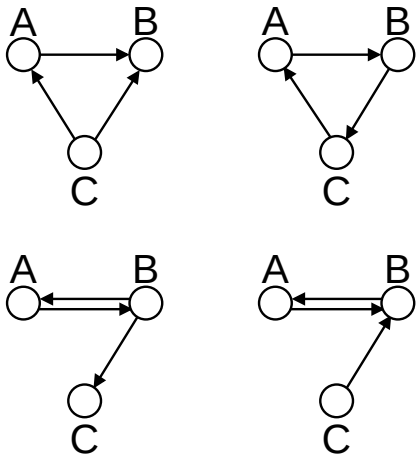


Figure 8: Possible unique arrangements of three species and three interactions excluding cannibalistic links. The connectance for each arrangement is the same but the corresponding structures represent vastly different ecological interactions, such as omnivory or tri-trophic chain

While these macro-scale measures provide insight into the general structure of a network, they may be masking potentially important variation in the sub-network, or meso-scale, structure. For example, consider a simple network of three species and three interactions. Excluding cannibalism, there are four different ways to arrange these interactions, all of which produce networks with the same level of connectance but contain very different meso-scale structures (Fig. 8). Previous work has shown that the arrangement of the interactions in the meso-scale structures can have important biological consequences, such as providing increased community persistence (Stouffer and Bascompte, 2010). Thus, in order to properly interpret the macro-scale measures of network structure, we first need to understand the variation present at the sub-network and species-level scales.

To quantify the sub-network structure of ecological networks, we turn to the concept of network motifs (Milo et al., 2002, 2004). Network motifs represent patterns of interactions between a small number of species. These motifs simplify the characterization of large net-

works and act as a bridge between the individual species and whole-network perspectives (Bascompte et al., 2005; Camacho et al., 2007; Stouffer et al., 2007). Any network can be decomposed into a unique set of motifs that can be thought of as the building blocks of the network. Importantly, the decomposition of a network into its unique set of motifs does not discard any information about the macro-scale structure of the network (Milo et al., 2002). In addition, some of these motifs represent important ecological interactions, such as apparent and exploitative competition (Stouffer and Bascompte, 2010) and have been shown to confer positive benefits to their networks (Holt, 1997; Stouffer and Bascompte, 2010).

Much of the work to date with network motifs has been conducted using trophic food-webs; that is, networks representing predators and prey (Bascompte et al., 2005; Camacho et al., 2007; Stouffer et al., 2007, 2012). Unfortunately, bipartite ecological networks such as plant-pollinator, plant-seed disperser, or host-parasite networks have been largely ignored from the motif perspective. Instead, nestedness or modularity have often been used to describe the organizational structure of empirical bipartite networks. While these measures have improved our understanding of some emergent properties (Bastolla et al., 2009; Memmott et al., 2004; Fortuna et al., 2010; Thébault and Fontaine, 2010), a great deal of structural variation is unaccounted for. Moreover, this structural variation can have important consequences both at the network and species levels (Saavedra et al., 2011).

Here, we propose a detailed examination of the meso-scale structure of bipartite ecological networks and how these structures are influenced by the macro-scale structure of the network. Specifically, we quantified the motif profiles and the participation of each species across motif profiles for simulated networks. Importantly, we found that at fixed values of connectance, nestedness, and modularity there was significant variation in the underlying meso-scale structure of networks. Finally, we found that macro-scale structures may be misleading when describing bipartite ecological networks and that care should be taken when used as the sole descriptor of an ecological community.

Methods

Network generation

We simulated bipartite ecological networks using the bipartite cooperation model developed by Saavedra et al. (2009). This model takes as input the number of row species, the number of column species, and the total number of links desired. For our networks, we randomly selected the number of row r and column c species from a range of values between 5 and 50 species, giving a minimum network size of $5x5$ and a maximum network size of $50x50$. In order to obtain networks that spanned a gradient of possible connectances, we set the number of links $l = (r * c * connectance)$, where connectance was selected from a range between the minimum connectance necessary for each species to have at least one interaction ($\frac{max(r,c)}{(r*c)}$) and 0.5. Following this process, we generated $20,000$ bipartite networks.

Network motifs

To quantify the motif profiles for our networks, we follow methods established in previous studies (Milo et al., 2002; Stouffer et al., 2007). Instead of focusing on three-species motifs, we instead expand our methodology following Baker et al. (2015) and calculated motif structures up to size five for all networks in this study, giving a total of 17 unique motifs (Supplementary material Appendix 3, Fig. A27). For each network n, we enumerated the frequency n_j with which motif j appeared in network n, which created a vector

$$\overrightarrow{n}_j = \{n_1, n_2, \ldots, n_{17}\} \ , \tag{5}$$

this vector is a multidimensional measure of the frequency with which each unique motif appears in each network and will be referred to as the "motif profile" for each network.

Species' participation in motifs

To measure the participation of each species across all motifs in a network, we used methods similar to those used in Baker et al. (2015) to quantify the network role of each species. To quantify the participation profile of each species (i) in network n based on the observed

motif frequencies, we enumerated the frequency $p_{ij|n}$ with which species i appears in each unique motif (j) in network n. Due to computational constraints, we restricted our participation calculations to motifs up to size 4. For all species i, this enumeration process created a vector

$$\overrightarrow{p}_{i|n} = \{p_{i1}, p_{i2}, \ldots, p_{i7}\}_n \ , \tag{6}$$

which can be thought of as a multidimensional measure of how that species arranges itself across the size 4 motif profile of each network.

Macro-scale network properties

For each network in our study, we quantified three whole-network measures of network structure: connectance, nestedness, and modularity. To measure the connectance of each network, we took the total number of links in the network and divided that by the product of the number of row and column species ($\frac{l}{(r*c)}$). Nestedness was measured using the metric based on overlap and decreasing fill (NODF; Almeida-Neto et al., 2008) which has a value between 0 (no nestedness) and 100 (perfect nestedness). Modularity was calculated following the community detection algorithm from Leicht and Newman (2008), which calculates quickly and has been shown to give similar results as other community detection algorithms (Leicht and Newman, 2008). Here, a value of 0 represents a network with no distinct groups, or modules, and a value of 1 represents a network composed of many independent modules that have no shared interactions.

Variation in network structure

In order to measure variation in the structure of our networks and how this variation was related to whole-network measures, we chose to use multi-variate distances. Multivariate distances have been used in a variety of analyses and are able to detect small variations between samples across multiple dimensions (Anderson, 2001; Anderson and Robinson, 2003; Baker et al., 2015). We compared the structure of networks at three different scales (whole-network, subnetwork, and species-level scales) in multivariate space to determine how much variation exists within our simulated networks.

First, we chose a whole-network measure of network structure, such as connectance, and organized all simulated networks in ascending order based on this structure (i.e., least to most connected). We then evenly divided our $20,000$ networks in to groups of 50, giving us 400 groups of 50 networks, each group with similar values of our whole-network structure of interest, i.e., connectance, nestedness, or modularity.

After the networks were organized, we calculated the multivariate distance to group centroid using a distance measure based on correlation. Here, the correlation between two vectors, e.g., the motif profile of two networks, can be thought of in terms of lines on a plain. If the two lines start at the same point and are travelling in the same direction then the correlation between them would be approximately 1. If, however, the lines start at the same point and travel in opposite directions, then the correlation between them would be approximately -1. In order to have non-negative values of distance, we took the correlation values and subtracted them from 1, giving a range of possible "correlation distances" between 0 if the profiles are identical and a value of 2 if they are completely different.

For each group of 50 networks, we calculated all pairwise correlation distances at three scales. At the whole-network scale, we created a profile for each network composed of the "unused" macro-scale network properties. For example, if we organized the networks by connectance, our whole-network profile would be composed of the: number of row species, number of column species, modularity, and nestedness of each network. At the meso-scale we used the motif profiles, and at the individual species scale we used the motif participation profiles for each network. We calculated the distance to group centroid for all networks in each group using the betadisper function from the vegan R package (R Core Team, 2015). Next, we calculated the mean distance to group centroid and standard error for each of our 400 groups of 50 networks. This approach provides us with a measure of variability at three scales for each network across a gradient of whole-network measures. This process was repeated two more times, once where we sorted the networks by nestedness and another where we sorted the networks by modularity, giving a total of three different views of the variability of network structure at varying scales.

Statistical analysis

To assess whether structural variation was influenced by the whole-network measure that the networks were sorted by (e.g., nestedness), we quantified the relationship between variation (mean distance to group centroid) and the mean of the whole-network measure for each group of 50 networks with a generalized additive model. Generalized additive models function in the same way that generalized linear models do, except the additive model replaces the linear form,

$$Y = \beta_0 + \beta_1 X_1 + \epsilon\,, \tag{7}$$

where Y is our response variable, β_0 is the intercept, $\beta_1 X_1$ is the effect of our explanatory variable on our response variable Y (e.g., the effect of nestedness on structural variation), with a smoothing function $s(\cdot)$. Thus, our equation becomes

$$Y = s_0 + s_1(X_1)\,, \tag{8}$$

where s_0 acts as the intercept and $s_1(X_1)$ acts as a smoothing function to allow for non-parametric model estimates (Hastie and Tibshirani, 1986). We used the *gam* function with a gaussian family and identity link function from the *mgcv* package in R 2.15.1 (R Core Team, 2015), which uses penalized regression splines (Wood and Augustin, 2002) to estimate the smoothness of the function $s_1(X_1)$ (Wood, 2004). Our models take the form

$$V = s_0 + s_1(X_1) + \epsilon\,, \tag{9}$$

where V is structural variation, measured as the mean distance to group centroid, and X_1 is the whole-network measure that the data were organized by, i.e., connectance, nestedness, or modularity. In order to determine if there were differences between scales (e.g., participation, motif, or whole-network) we added another parameter *scale* to the generalized additive model

$$V = s_0 + scale + s_1(X_1) + \epsilon,\,, \tag{10}$$

where *scale* is a categorical variable representing the scale of the analysis, i.e., species-level (motif participation), sub-network (motifs), and macro (whole-network measures) scales. As before, $s_1(\cdot)$ represents a smoothing function and X_1 represents the the whole-network measure the networks were sorted by. Importantly, only X_1 is smoothed in this analysis, *scale* was not. The results of this model were analysed using the *aov* (analysis of variance) function in R 2.15.1 (R Core Team, 2015).

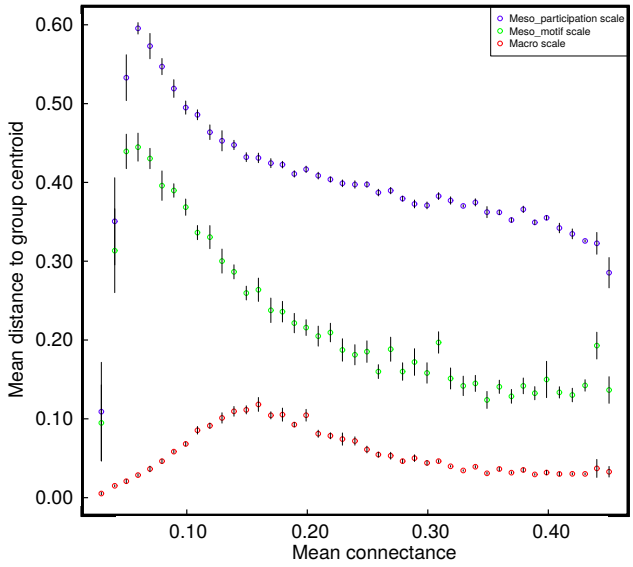


Figure 9: Network variation (mean distance to group centroid) vs. mean connectance for all networks. Points represent groups of networks and error bars represent ± 1 standard error. Whole-network observations (red - bottom) show little variation when compared to sub-network (green - middle) and species-level scales (blue - top).

Across our 20,000 simulated networks, mean connectance was 0.23 (min = 0.02, max = 0.5), mean nestedness was 47.70 (min = 0.00, max = 93.87), mean modularity was 0.5476 (min = 0.11, max = 0.98), and finally, the mean number of species in these networks was 54.76 with a minimum number of species of 10 ($5x5$ matrix) , and a maximum number of species of 100 ($50x50$ matrix).

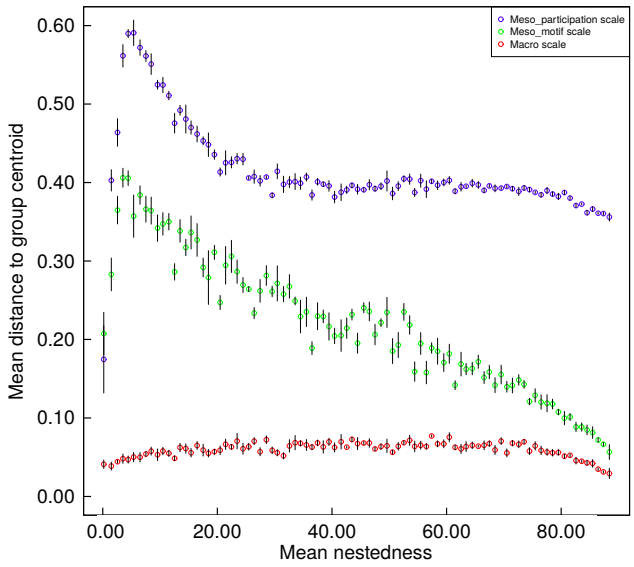


Figure 10: Network variation (mean distance to group centroid) vs. mean nestedness for all networks. Points represent groups of networks and error bars represent ± 1 standard error. Whole-network observations (red - bottom) show little variation when compared to sub-network (green - middle) and species-level scales (blue - top).

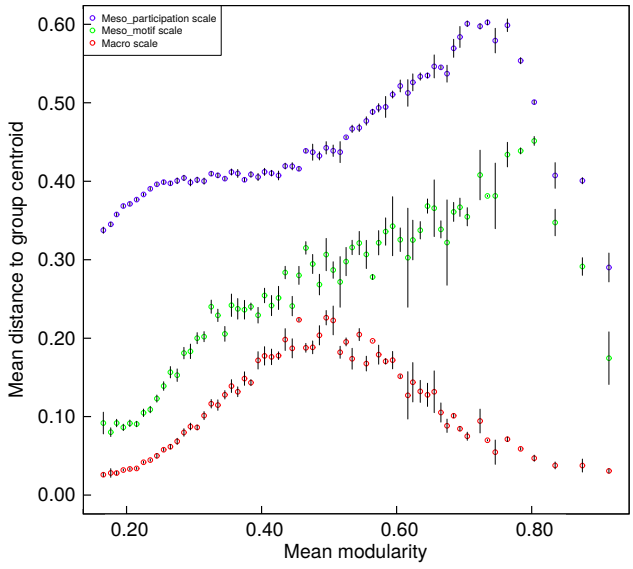


Figure 11: Network variation (mean distance to group centroid) vs. mean modularity for all networks. Points represent groups of networks and error bars represent ±1 standard error. Whole-network observations (red - bottom) show little variation when compared to sub-network (green - middle) and species-level scales (blue - top).

At the species-level, the mean variation of networks when organized by connectance was 0.4018 (se +/- 0.0126; Fig. 9). The mean variation when organized by nestedness was 0.4149 (se +/- 0.0062; Fig. 10) and the mean variation when organized by modularity was 0.4515 (se +/- 0.0093; Fig. 11). At the sub-network scale, the mean variation when organized by connectance was 0.2233 (se +/- 0.0148; Fig. 9).

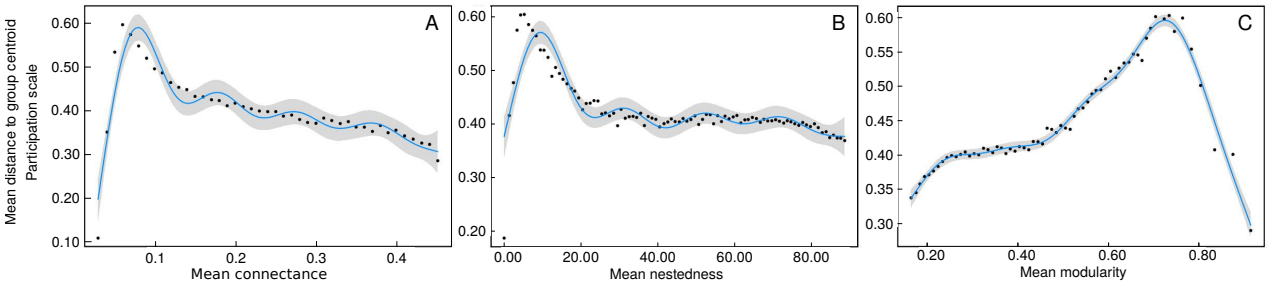


Figure 12: Generalized additive model prediction for species-level variation. Grey regions represent 95% confidence intervals and the blue line represents the predicted relationship between participation scale network variation and mean connectance (**A**; $R^2 = 0.845$), mean nestedness (**B**; $R^2 = 0.704$), and mean modularity (**C**; $R^2 = 0.979$).

When organized by nestedness, mean variation at the sub-network scale was 0.2185 (se +/- 0.0091; Fig. 10) and when organized by modularity, mean variation was 0.2631 (se +/- 0.0121; Fig. 11). Finally, at the whole-network scale, the mean variation when organized by connectance was 0.0566 (se +/- 0.0046; Fig. 9). The mean variation when organized by nestedness was 0.0595 (se +/- 0.0010; Fig. 10), and the mean variation when organized by modularity, was 0.1178 (se +/- 0.0077; Fig. 11).

To assess the relationship between network variation and whole-network measures of network structure, we used generalized additive

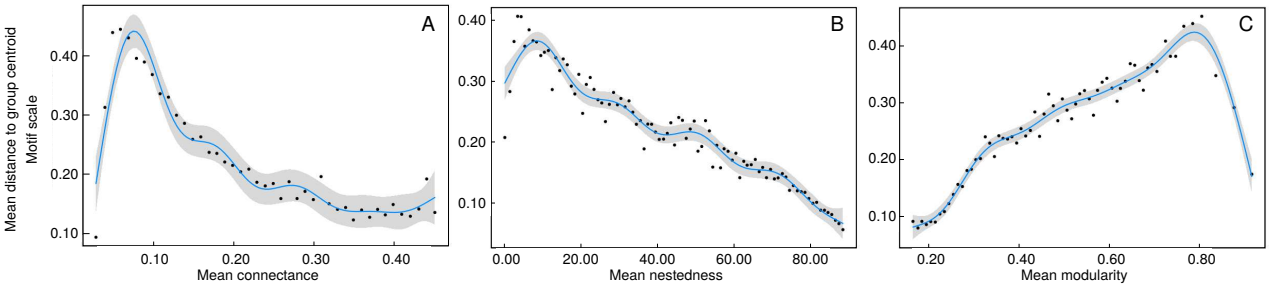


Figure 13: Generalized additive model prediction for sub-network variation. Grey regions represent 95% confidence intervals and the blue line represents the predicted relationship between participation scale network variation and mean connectance (**A**; $R^2 = 0.902$), mean nestedness (**B**; $R^2 = 0.930$), and mean modularity (**C**; $R^2 = 0.968$).

models. At the participation scale, we found that mean connectance, nestedness, and modularity were all significantly related to the variation observed in network structure ($p =< 0.0001$, $R^2 = 0.845$; $p < 0.0001$, $R^2 = 0.704$; $p < 0.0001$, $R^2 = 0.979$, respectively; Fig. 12).

Similarly, at the sub-network scale, we found that mean connectance, nestedness, and modularity were all significantly related to the variation observed in network structure ($p =< 0.0001$, $R^2 = 0.902$; $p < 0.0001$, $R^2 = 0.930$; $p < 0.0001$, $R^2 = 0.968$, respectively; Fig. 13). At the whole-network scale only connectance was significantly related to the variation observed in network structure ($p = 0.023$, $R^2 = 0.985$; Fig. 14).

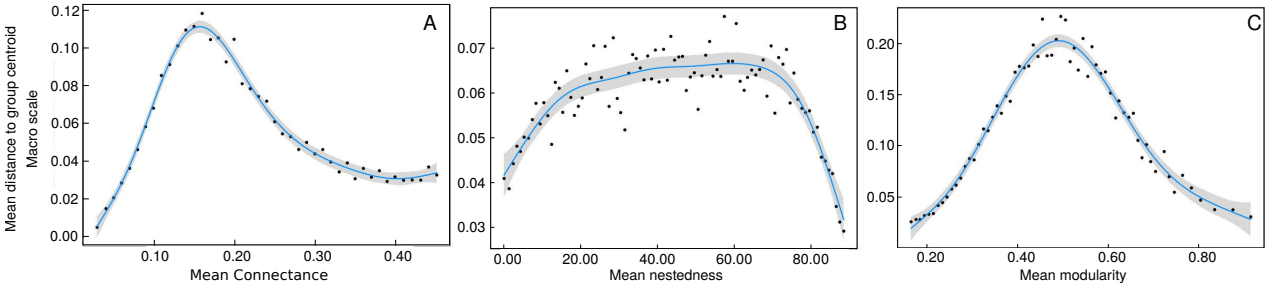


Figure 14: Generalized additive model prediction for whole-network variation. Grey regions represent 95% confidence intervals and the blue line represents the predicted relationship between participation scale network variation and mean connectance (**A**; $R^2 = 0.985$), mean nestedness, and mean modularity. At the whole-network scale, only connectance was significantly related to mean variation in network structure.

There was also a significant difference between the scale of network structure and variation when organized by connectance, nestedness, and modularity ($F_{2,125} = 335.75$, $p < 0.0001$; $F_{2,263} = 1300.3$, $p < 0.0001$; $F_{2,188} = 443.2$, $p < 0.0001$, respectively).

Discussion

Overall, we found that at fixed levels of connectance, nestedness, and modularity, the motif profiles of networks and the distribution of species across those profiles showed remarkable dissimilarity, suggesting that networks displaying similar macro-scale structural measures can be composed of vastly different meso-scale structures. (see Fig. 12, 13, 14).

When measuring variation at different scales, we observed that as the scale of network organization decreased (i.e., as we moved from the whole-network to the species-level) we found that the amount of variation increased substantially. We also observed significant differences in network variation based on the whole-network organization of links and the scale of variation. For example, if we focus on the pattern of variation with respect to connectance, at all three scales, we see that variation has a non-parametric relationship with connectance (Fig. 9). This complex relationship is likely related to the number of possible networks that can exist at the extreme values of connectance (Poisot and Gravel, 2014).

Poisot and Gravel (2014) showed that based on the connectance of the network, there exists a "network space" that imposes strict limitations on what networks are possible (Fig. 7). Our results show that at the lowest values of connectance, network variability is low, suggesting that the networks were all very similar. Then, as connectance increased, the amount of variation in network structure also increased. Finally, after a certain value of connectance (approximately 0.15) network variation began to decrease (Fig.: 12A., 13A., and 14A). Interestingly, previous studies have found that increased species diversity is associated with decreased connectance (Schmid-Araya et al., 2002; Canard et al., 2012). While it is beyond the scope of this study, it would be interesting to determine if we see the same relationship between connectance and network variation in empirical networks and if that pattern were correlated with increased species diversity, as previous studies have suggested.

The variation in network structure observed when organized by nestedness was highest at the lowest levels of nestedness (Fig.: 12B., 13B., and 14B.). If we consider nestedness as a measure dictating a certain, rigid pattern of organization within a network, then it makes sense that at the lowest values of nestedness, we would observe the most variation in network structure. Then, as we pro-

gressively get more rigid with our interaction organization, our available network variation decays, until we are left with few possible ways in which the interactions can come together to meet a particular value of nestedness. Interestingly, this pattern may offer some support for other theoretical and empirical work that has shown that increased nestedness increases the stability and resilience of certain types of bipartite networks, mainly mutualistic networks (Olesen et al., 2007; Thébault and Fontaine, 2010; Fortuna et al., 2010), though recent work casts doubt on the nestedness-stability debate (Strona and Veech, 2015). The decreased variation of the network may suggest a more stable "network state", which may be more resistant to outside disturbances.

Finally, the variation in network structure when organized by modularity showed the opposite pattern to that of nestedness. This result reinforces the idea that nestedness and modularity are two-sides of a coin, where you cannot have high levels of modularity and high levels of nestedness (Fortuna et al., 2010). We see the lowest level of network variation at the lowest value of modularity, and as modularity increases so does the variation present within the networks, up to a certain point (Fig.: 12C., 13C., and 14C.). In the context of an ecological community, at the lowest levels of modularity all species interact with each other, suggesting a relatively low amount of possible variation. However, as you increase modularity, which subsequently is associated with a decrease in connectance, the number of unique species-species combinations starts to increase, which leads to an increase in the variation of network structure. Other studies have suggested that increased modularity is associated with increased interaction specialisation (Cagnolo et al., 2011; Strona and Veech, 2015). For example, host-parasitoid networks tend to be modular because parasitoid species prefer specific host species, which narrows the number of possible interactions of the network (Cagnolo et al., 2011). It follows that increased interaction specialization could be associated with an increase in the variation of network structure as there are more unique interaction combinations available.

While the patterns observed in network variation were, for the most part, consistent across scales, such as the parabolic relationship with connectance, negative linear relationship with nestedness, or the positive linear relationship with modularity, the magnitude of the variation described by the patterns was quite different. As we move from a macro-scale view to an individual species view the amount of observed variation increases, in some cases by an order of magnitude (Figs. 9, 10, 11). It is this increase in variation that underlies

the problem of classifying a network by its macro-scale properties alone. Classifying a network by a value of nestedness or modularity, outside of the extreme cases of those measures, can obscure a wealth of potential information. We have demonstrated that at a given value of connectance, nestedness, or modularity networks can be composed of vastly different structures. This result also suggests that we should consider all measures of network structure wherever possible, as single measures can be misleading (Thébault and Fontaine, 2010; Fortuna et al., 2010; Cagnolo et al., 2011)

While considering only whole-network structural properties ignores the majority of available information about network structure, determining the species-level structure of a network is much more computationally intensive. Depending on the size and connectance of the network in question, the additional level of detail provided by motif participation may take minutes to weeks to obtain. As a balance between the loss of information implied by using only whole-network properties and the time and resources required to obtain species-level information, we suggest using a meso-scale approach. The motif profile of a network captures more of the variation in network structure than whole-network properties, such as connectance, while still being computationally "light" enough for rapid analysis. It therefore provides a valuable lens through which we can explore the intricacies of ecological network structure.

Conclusion

In this thesis, we have investigated variation in ecological network structure from both an empirical and theoretical perspective. First, we examined the fidelity of species' roles in a highly variable host-parasitoid community in Southern Finland. Second, we took a theoretical approach to explore the relationship between different scales of network structure and network organization. Taken together, the results of these studies have implications for the study of ecological network structure and our understanding of network organization.

Fidelity of species' roles

In our analysis of an empirical host-parasitoid ecological community, we found that species' roles for host and parasitoid species showed signs of fidelity (i.e., little variation) at the species, network, and temporal scales. We also found that for host species, network specialization was positively related to host role fidelity such that more specialized networks showed more role fidelity than less specialized networks. This may indicate that there is less niche overlap in those networks and that the turnover of species may be more predictable. We found that the temporal fidelity of parasitoid roles was intimately connected with host species turnover such that increased turnover of host species between years was positively related to parasitoid role fidelity. This suggests that species' roles are related to the roles of their interaction partners in counter-intuitive ways.

Our results in this chapter further suggest that species' roles are an intrinsic species characteristic, supporting previous research showing that phylogenetically-related species showed similar roles (Stouffer et al., 2012). In the context of the work discussed in "*Species' roles in food webs show fidelity across a highly variable oak for-*

est", it would appear that species fidelity imposes constraints on the community and overall food-web structure. These structural constraints should improve predictions about the interaction niche of a particular species as well as many other species in the network. At the network level, we found that the roles in any given network were more similar to each other than to the roles found in other networks. Interestingly, previous research on this system found that the networks themselves maintained their structure across the landscape (Kaartinen and Roslin, 2011), suggesting that networks were very similar from a macro-scale network structure perspective. However, in order for our results to be fully consistent with Kaartinen and Roslin (2012) there must be multiple ways in which species' roles can be combined to produce *equivalent* macro-scale network structure. This theory aligns perfectly with results obtained in *"A meso-scale approach to understanding macro-scale measures of ecological networks"*, where we show that networks with similar macro-scale structures can have highly variable motif profiles. Finally, we found that species' roles were consistent between years at sites. This work supports the results of Kaartinen and Roslin (2012), who found that the quantitative structure of the food-webs changed very little between years. While we observed role fidelity between sites, there was on average 50% species turnover and 70% interaction turnover between years. Temporal fidelity provides the expectation, then, that nearly all species that leave the network between years are replaced by new species with a comparable role. Coupled with the predictability of species' roles across years, this means that changes in network composition between years may be predictable based on the role structure of the community.

Variation in network structure

Quantifying the variation of bipartite ecological networks depends on the number of interactions and how those interactions are organized within the network. While this basic concept is not new, here we have explicitly shown that variation in ecological networks depends on the scale at which those networks are analysed as well as on their size and complexity. This demonstrates that the scale at which we categorize networks will affect the conclusions that can be drawn.

We found that the relationship between network connectance and structural variation was complex, with extreme measures of connectance corresponding to low levels of structural variation in the

network and moderate values of connectance resulting in the highest levels of network variation. This pattern follows the same pattern that Poisot and Gravel (2014) found when exploring the range of possible networks based on the number of available links in the network. In addition, the lowest values of nestedness were related to networks with the highest levels of structural variation, which suggests that nestedness imposes strict limitations on network structure. In contrast, we found that the modularity of the network was linearly related to structural variation, with lowest levels of modularity aligning with the lowest levels of structural variation and higher levels of modularity related to higher levels of structural variation. The conflicting influences of nestedness and modularity on network structure have been explored previously (Fortuna et al., 2010; Thébault and Fontaine, 2010) and our analysis supports the theory that increased levels of nestedness are directly related to decreased levels of modularity. Finally, we found that these results were consistent across three scales of network structure: whole-network, sub-network, and species-level. However, the magnitude of variation was dramatically different with the species-level scale (participation) consistently showing the most variation and the whole-network structure consistently showing the least.

Implications for theory and application

"Species' roles in food webs show fidelity across a highly variable oak forest" and *"A meso-scale approach to understanding macro-scale measures of ecological networks"* bring together an empirical and theoretical view of ecological network structure. From the theoretical context, we demonstrate the inherent limitations of some measures of ecological network structure. It has been argued before that we must consider more than a single macro-scale measure when describing ecological networks (Fortuna et al., 2010; Thébault and Fontaine, 2010; Cagnolo et al., 2011), however, most such arguments centred around combining several whole-network measures of structure. By neglecting finer-scale variation in ecological networks, even combining several large-scale measures may not capture the mechanisms driving community structure. For example, in *"Species' roles in food webs show fidelity across a highly variable oak forest"*, we demonstrate that species' roles provide a wealth of additional information about the host-parasitoid community, information that was previously unknown when viewing the network from a macro-scale only context (Kaartinen and Roslin, 2011, 2012). By addressing species-level

structure in empirical networks, we show that variation in network structure appears to be driven by species-level characteristics, adding yet another level of complexity to the understanding of ecological networks.

If we want to gain a more in-depth understanding of ecological networks, we must first quantify network structure in a more detailed and refined manner. Moving from whole-network perspectives towards individual species perspectives offers the most detailed account of network structure. However, we cannot get lost in theory, in *"Species' roles in food webs show fidelity across a highly variable oak forest"*, we show that once you break down the network into the species-level components, there is still a tremendous amount of biology directing the structure of the community. What we do know is that related species should tend towards similar interactions in a network and that phylogenetically-related species should have similar interaction characteristics no matter where they exist globally (Stouffer et al., 2012). Our results take this one step further and suggest the possibility that species' roles may adhere to a strict pattern, such that if a species with a particular role leaves a network, any replacement species entering the network would have to have a similar interaction profile. While this is just a theory, it would be an intriguing mechanism by which ecological communities could maintain ecological function and stability when confronted with disturbances.

Future directions

There are many different directions one could pursue based on this research. In both chapters, we only considered bipartite network types (e.g., plant-pollinator), forgoing application to traditional unipartite food-webs (e.g., predator-prey). Expanding both analyses to incorporate multiple types of ecological networks would be an interesting exercise and would reveal how well our results apply to different systems. In addition, we focused entirely on binary interaction networks, with no analyses considering quantitative interaction structure. The addition of quantitative interactions increase the complexity of the network but also provide a better match to natural systems. The simulated networks we used have been shown to mimic the structure of empirical networks (Saavedra et al., 2011), but it would be interesting to see how well our results hold when using only empirical networks.

In *"Species' roles in food webs show fidelity across a highly variable oak forest"*, we focused on a single host-parasitoid community. Branching this same analysis out to additional host-parasitoid as well as other bipartite communities would be extremely interesting, as we know that there are structural differences between antagonistic networks (like the host-parasitoid networks used here) and mutualistic networks (e.g., plant-pollinator). If our results were to hold with the addition of new communities and network types, then they may provide a meso-scale platform from which we can develop predictions about ecological communities. Additionally, as we learn more about the contributions of individual species to the structure and variation of ecological networks, we will be better suited to identify *network critical* species (i.e., species that act as hubs or who's removal causes secondary extinctions within the network), based on the patterns of their interactions alone. This would be a large jump for network theory and would provide detailed information to direct conservation efforts in systems that may be under threat.

In *"A meso-scale approach to understanding macro-scale measures of ecological networks"*, we demonstrated that in simulated ecological networks, variation in structure was associated with the patterns of organisation and the number of interactions of the network. Collecting equivalent empirical datasets would be an ideal situation from which we could compare not only the accuracy of the model, which has been shown to be quite good, but also if the type of network plays a role in restricting structural variation. In addition, it would be interesting to explore network stability with different motif profiles to determine if certain arrangements of motifs confer different advantages or disadvantages to a network. Finally, there are many additional ecological models that could be incorporated into this type of study, such as models that produce quantitative networks, or even probabilistic models that may produce networks with different motif structures. The addition of more data and a broader selection of models may provide unique insights to the overall structure and variation of ecological networks.

Conclusion

While there is a wealth of research on ecological network structure, specifically on the structure of bipartite network structure, there are still gaps in our knowledge. Here, we found that network variation depends not only on the scale of measure, the number of interactions,

or their organisation, but also on the particular biology of the species making up the network. The relationship between individual species and network structure is more complex than originally thought, to the extent that particular species may be able to impose structural rigidity on the community network, preventing variation that would otherwise take place over a landscape or through time. The research presented here should be viewed as an introduction to the concept of meso-scale network approaches to quantifying community structure. The insights presented in these chapters create a framework from which we can begin to understand the relationship between different scales of network structure and how these scales can be used to as a prediction platform for furthering our understanding of ecological community structure.

Supplementary Material – Species' roles in food webs show fidelity across a highly variable oak forest

Appendix 1

Species distribution across sites and networks

Species were widely distributed across the sites and interaction networks in the empirical data, with some species appearing very frequently and others rarely. Figures A1 and A2 show the presence and absence of all host and parasitoid species across all sites and networks.

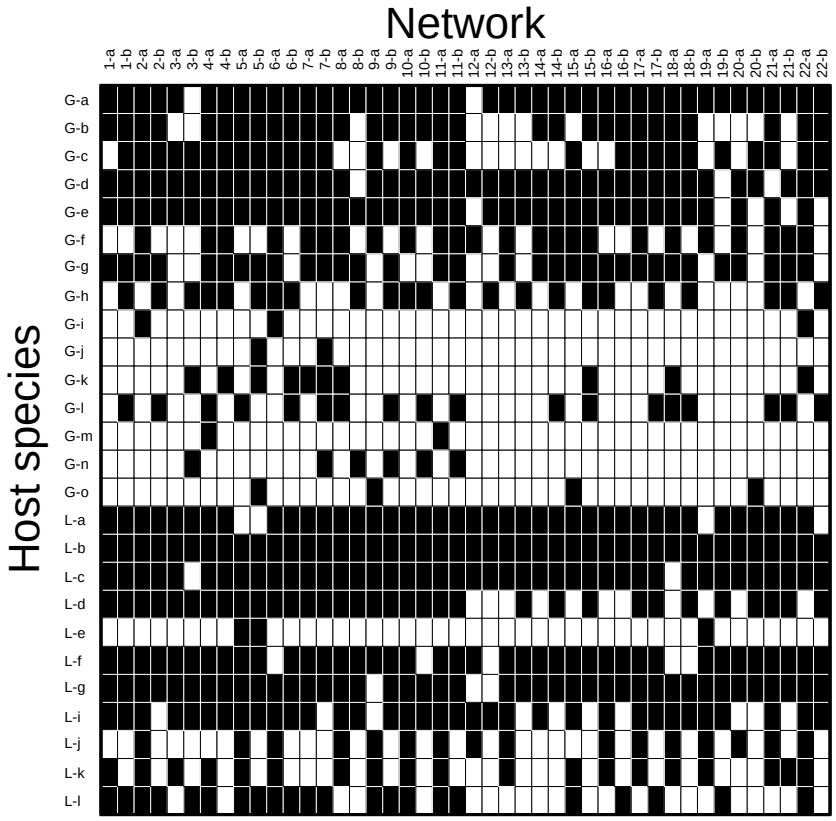


Figure 15: Graphical representation of the distribution of each host species across all networks. Networks are labelled by site with "a" representing the 2006 network and "b" representing the 2007 network. Colours indicate the presence (black square) or absence (white square) of the host at a particular site. Host species labels are organized by guild (G for galler and L for leafminer species) and are sorted in order of decreasing abundance within each guild.

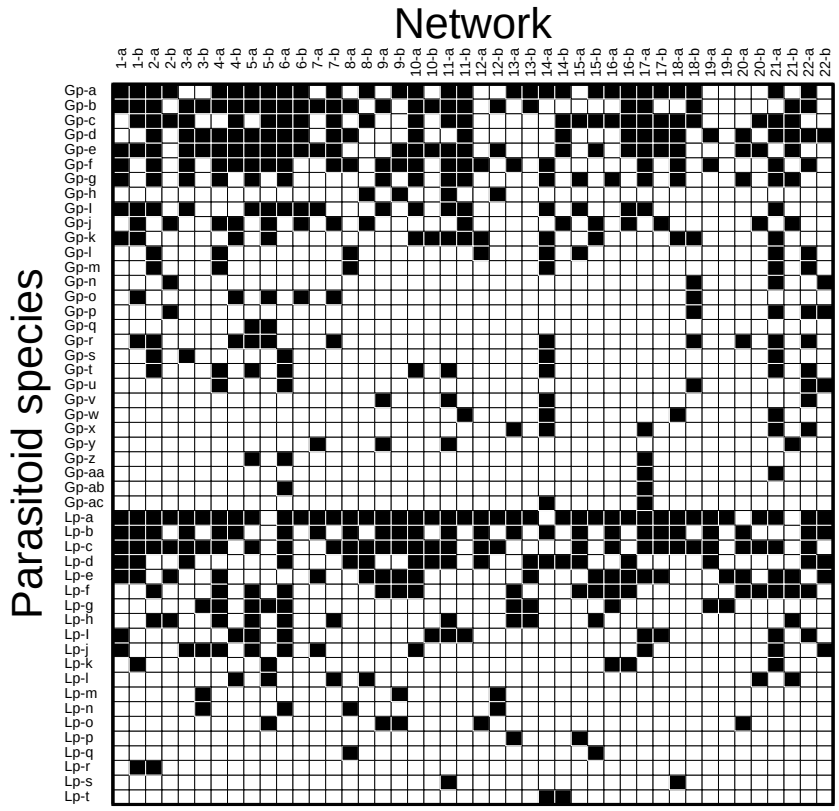


Figure 16: Graphical representation of the distribution of each parasitoid species across all networks. Networks are labelled by site with "a" representing the 2006 network and "b" representing the 2007 network. Colours indicate the presence (black square) or absence (white square) of the parasitoid at a particular site. Parasitoid species labels are organized by guild (Gp for galler parasitoid and Lp for leafminer parasitoid species) and are sorted in order of decreasing abundance within each guild.

Appendix 2

Robustness of our results to the use of qualitative interaction networks

In the analysis presented in the main text, we reduced the quantitative empirical networks to their binary equivalent. By doing so, it was possible that we ended up overemphasizing the contributions of rare species to the fidelity of species' roles. To test if our fidelity analyses were indeed influenced by rare species in this way, we tested the robustness of our results by comparing them to what we would expect under a statistical resampling of the empirical quantitative networks. Rather than assume all interactions are equiprobable irrespective of their empirically-observed intensity, the resampled networks represent a weighting proportional to the actual field data.

For each empirical network, the resampling procedure works as follows. First, we randomly selected a host species i with a probability given by its observed relative abundance (compared to all host species). Next, we randomly selected a parasitoid species j with probability given by its proportional attack rate on host i (i.e., its attack rate divided by the total number of attacks on host i from all parasitoid species). We then added an interaction between host i and parasitoid j to the "resampled" network. We repeated this process until the resampled network had the exact same number of quantitative interactions as the empirical network. Throughout this process, species (and interactions) that are more abundant in the empirical network will have a higher probability of appearing in the resampled networks, and rare species (or interactions) will have a lower probability of appearing (Fig. 17- 38).

We conducted the resampling procedure 999 times for the complete set of empirical networks. For each of these, we then calculated species, network, and temporal fidelity as detailed in the main text to create a null distribution of each p-value associated with the different levels of role fidelity (D'Agostino and Stephens, 1986). To test the robustness of our original conclusions, we compared the p-values from the qualitative networks to those from the resampled distributions to assess whether the qualitative results were statistically different from results obtained from quantitative networks.

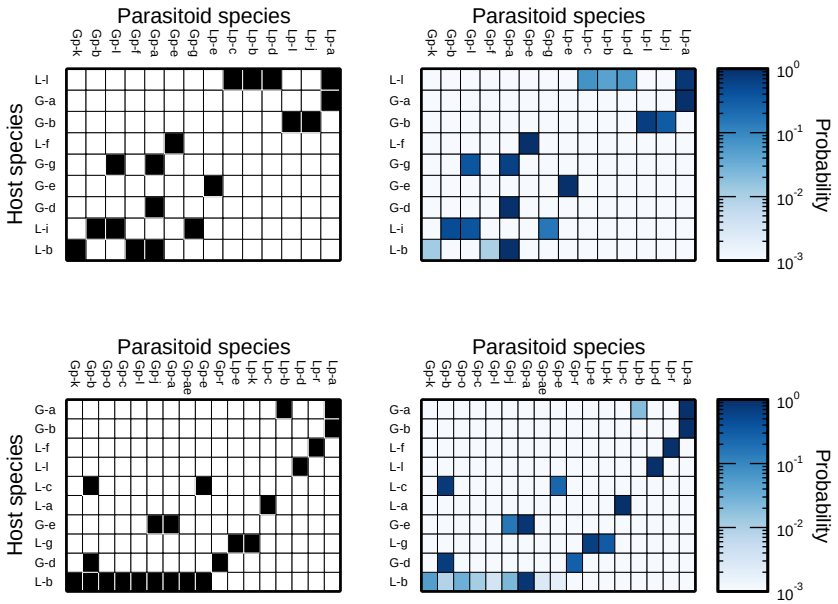


Figure 17: Graphical representation of the qualitative interaction network (left) and the mean of all 999 resampled networks (right) for site 1 in 2006 (top) and 2007 (bottom). Each cell represents a possible interaction between a host species and parasitoid species. In the qualitative network, a black cell represents the presence of an interaction whereas white represents its absence. In the resampled network, each cell is shaded according to the probability that the interaction appeared in the resampled networks, with the colours as indicated in the colorbar at right.

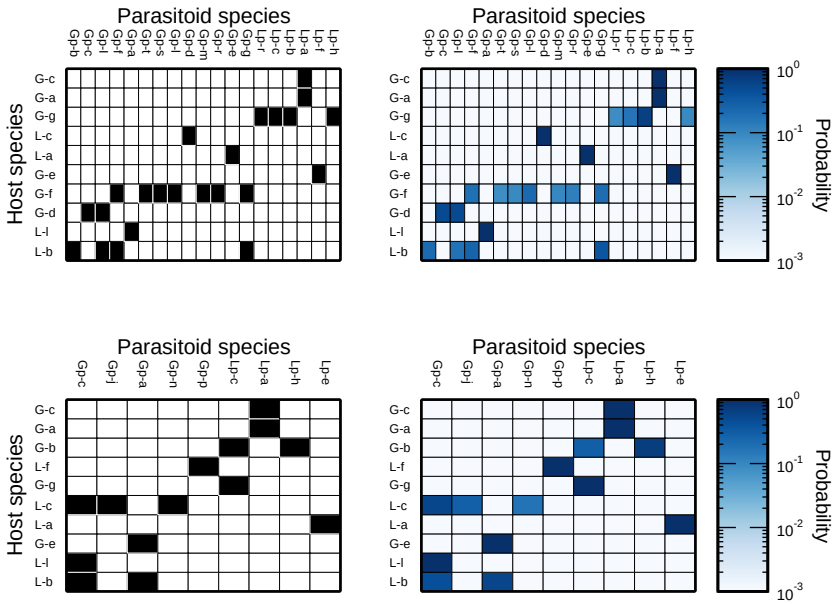


Figure 18: Graphical representation of the qualitative interaction network (left) and the mean of all 999 resampled networks (right) for site 2 in 2006 (top) and 2007 (bottom). Each cell represents a possible interaction between a host species and parasitoid species. In the qualitative network, a black cell represents the presence of an interaction whereas white represents its absence. In the resampled network, each cell is shaded according to the probability that the interaction appeared in the resampled networks, with the colours as indicated in the colorbar at right.

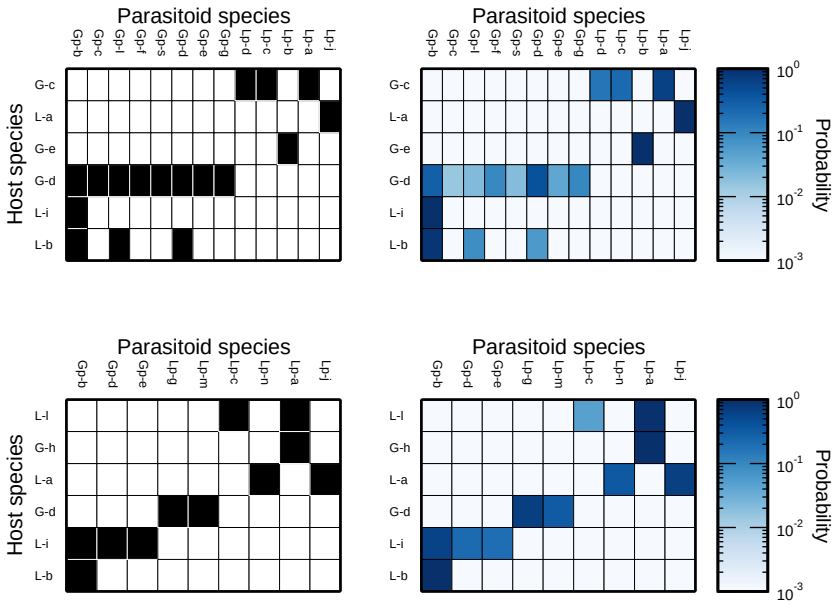


Figure 19: Graphical representation of the qualitative interaction network (left) and the mean of all 999 resampled networks (right) for site 3 in 2006 (top) and 2007 (bottom). Each cell represents a possible interaction between a host species and parasitoid species. In the qualitative network, a black cell represents the presence of an interaction whereas white represents its absence. In the resampled network, each cell is shaded according to the probability that the interaction appeared in the resampled networks, with the colours as indicated in the colorbar at right.

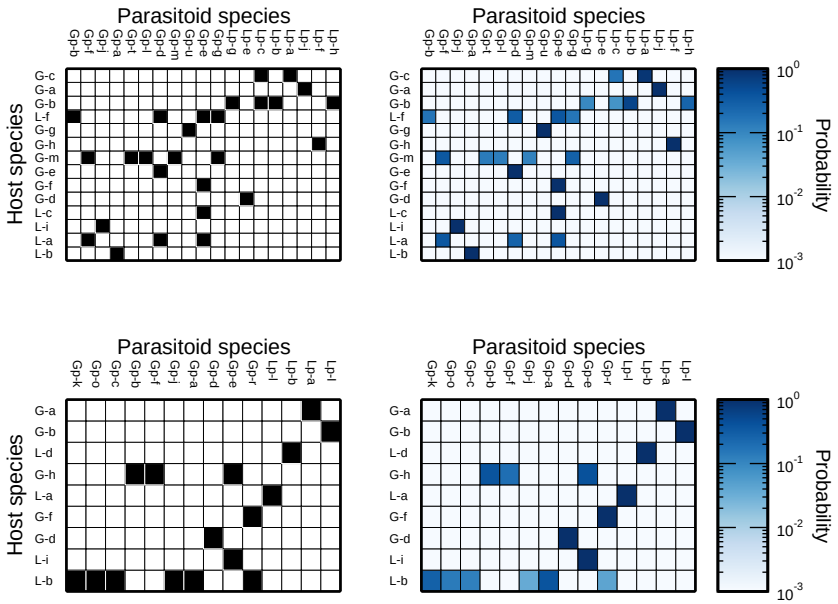


Figure 20: Graphical representation of the qualitative interaction network (left) and the mean of all 999 resampled networks (right) for site 4 in 2006 (top) and 2007 (bottom). Each cell represents a possible interaction between a host species and parasitoid species. In the qualitative network, a black cell represents the presence of an interaction whereas white represents its absence. In the resampled network, each cell is shaded according to the probability that the interaction appeared in the resampled networks, with the colours as indicated in the colorbar at right.

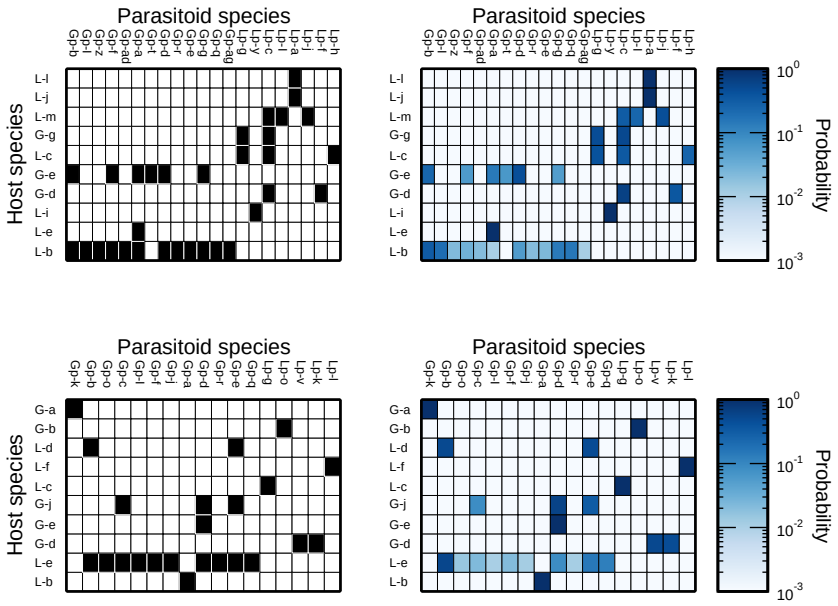


Figure 21: Graphical representation of the qualitative interaction network (left) and the mean of all 999 resampled networks (right) for site 5 in 2006 (top) and 2007 (bottom). Each cell represents a possible interaction between a host species and parasitoid species. In the qualitative network, a black cell represents the presence of an interaction whereas white represents its absence. In the resampled network, each cell is shaded according to the probability that the interaction appeared in the resampled networks, with the colours as indicated in the colorbar at right.

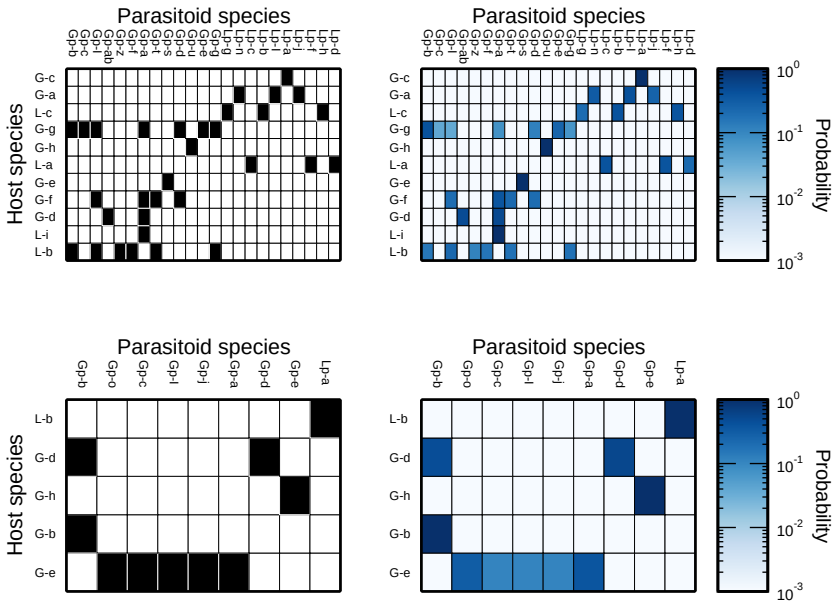


Figure 22: Graphical representation of the qualitative interaction network (left) and the mean of all 999 resampled networks (right) for site 6 in 2006 (top) and 2007 (bottom). Each cell represents a possible interaction between a host species and parasitoid species. In the qualitative network, a black cell represents the presence of an interaction whereas white represents its absence. In the resampled network, each cell is shaded according to the probability that the interaction appeared in the resampled networks, with the colours as indicated in the colorbar at right.

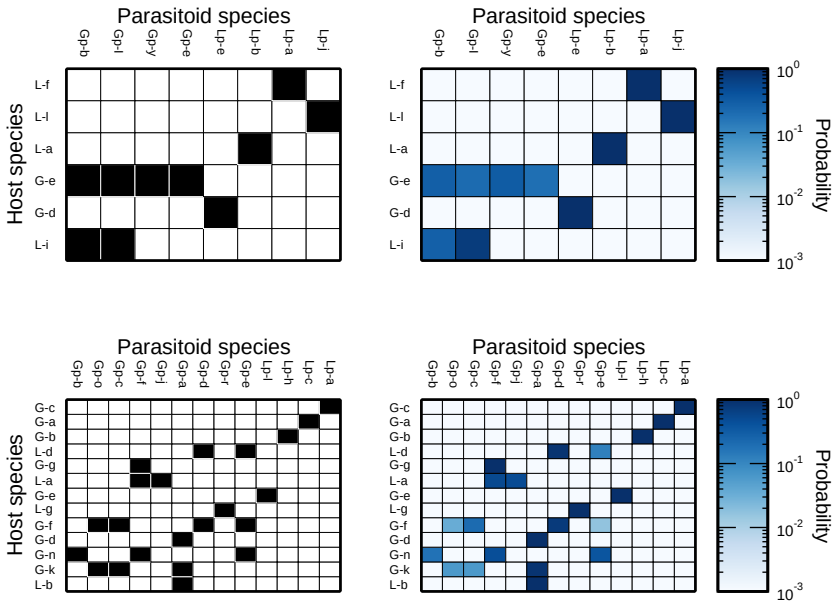


Figure 23: Graphical representation of the qualitative interaction network (left) and the mean of all 999 resampled networks (right) for site 7 in 2006 (top) and 2007 (bottom). Each cell represents a possible interaction between a host species and parasitoid species. In the qualitative network, a black cell represents the presence of an interaction whereas white represents its absence. In the resampled network, each cell is shaded according to the probability that the interaction appeared in the resampled networks, with the colours as indicated in the colorbar at right.

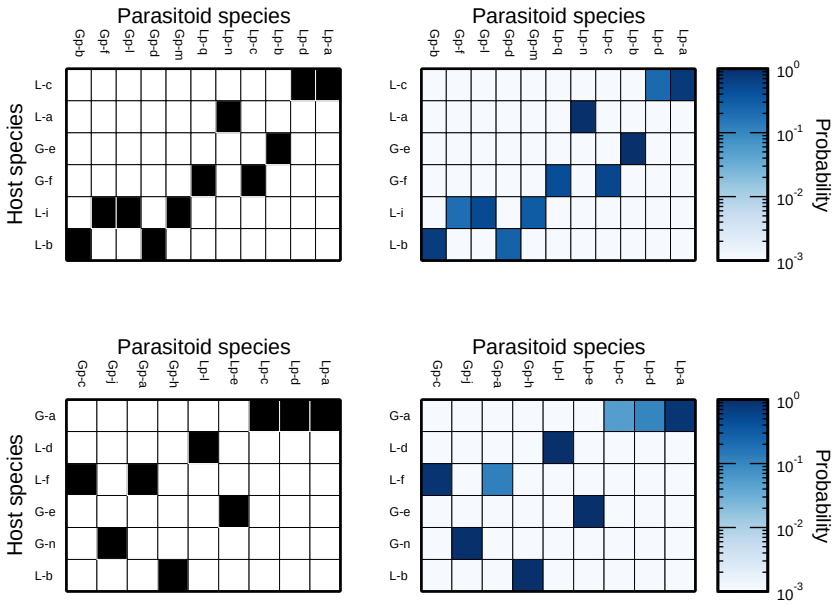


Figure 24: Graphical representation of the qualitative interaction network (left) and the mean of all 999 resampled networks (right) for site 8 in 2006 (top) and 2007 (bottom). Each cell represents a possible interaction between a host species and parasitoid species. In the qualitative network, a black cell represents the presence of an interaction whereas white represents its absence. In the resampled network, each cell is shaded according to the probability that the interaction appeared in the resampled networks, with the colours as indicated in the colorbar at right.

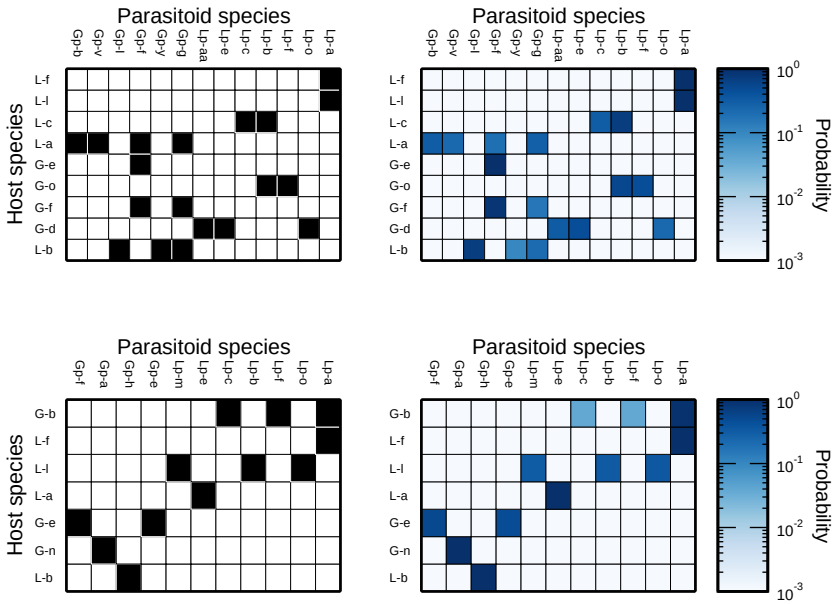


Figure 25: Graphical representation of the qualitative interaction network (left) and the mean of all 999 resampled networks (right) for site 9 in 2006 (top) and 2007 (bottom). Each cell represents a possible interaction between a host species and parasitoid species. In the qualitative network, a black cell represents the presence of an interaction whereas white represents its absence. In the resampled network, each cell is shaded according to the probability that the interaction appeared in the resampled networks, with the colours as indicated in the colorbar at right.

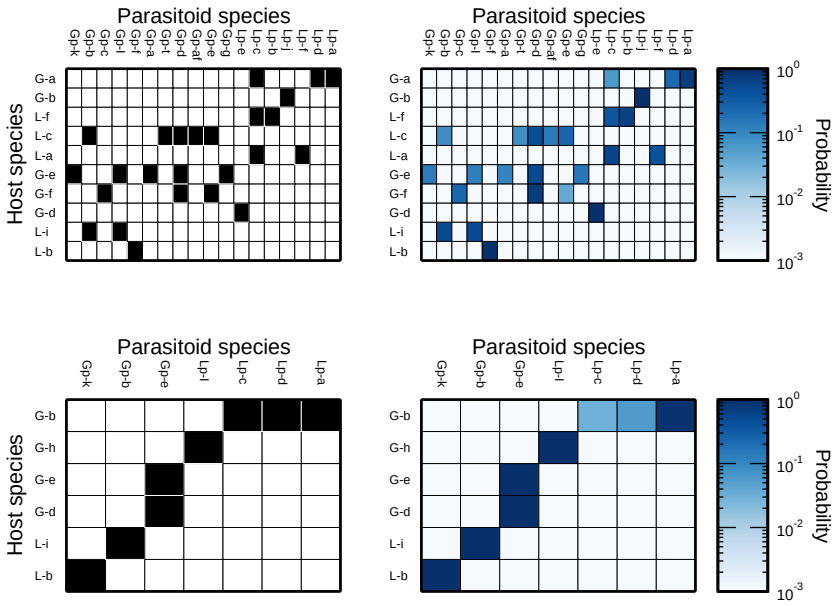


Figure 26: Graphical representation of the qualitative interaction network (left) and the mean of all 999 resampled networks (right) for site 10 in 2006 (top) and 2007 (bottom). Each cell represents a possible interaction between a host species and parasitoid species. In the qualitative network, a black cell represents the presence of an interaction whereas white represents its absence. In the resampled network, each cell is shaded according to the probability that the interaction appeared in the resampled networks, with the colours as indicated in the colorbar at right.

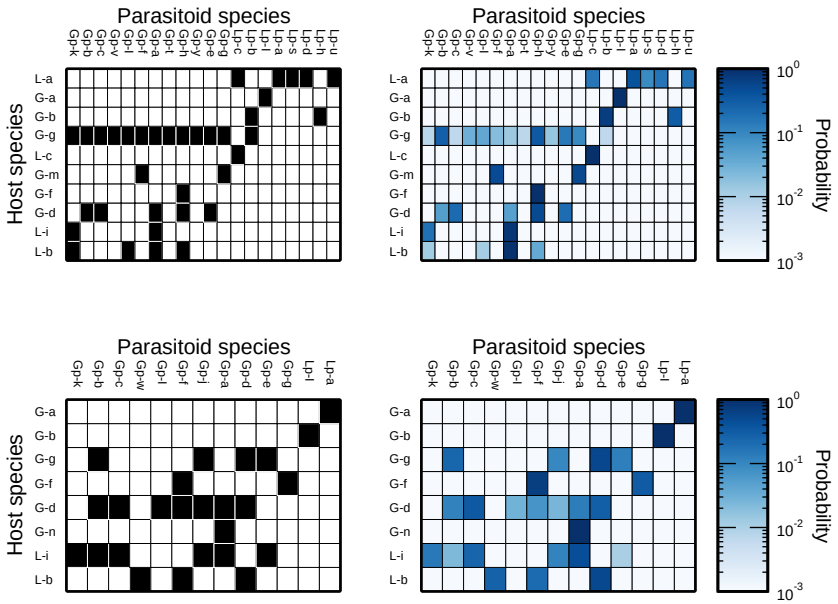


Figure 27: Graphical representation of the qualitative interaction network (left) and the mean of all 999 resampled networks (right) for site 11 in 2006 (top) and 2007 (bottom). Each cell represents a possible interaction between a host species and parasitoid species. In the qualitative network, a black cell represents the presence of an interaction whereas white represents its absence. In the resampled network, each cell is shaded according to the probability that the interaction appeared in the resampled networks, with the colours as indicated in the colorbar at right.

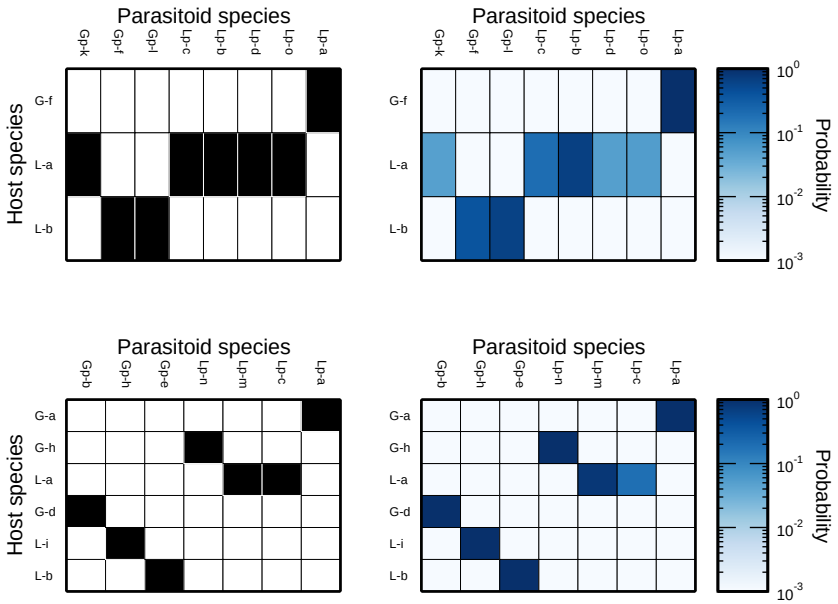


Figure 28: Graphical representation of the qualitative interaction network (left) and the mean of all 999 resampled networks (right) for site 12 in 2006 (top) and 2007 (bottom). Each cell represents a possible interaction between a host species and parasitoid species. In the qualitative network, a black cell represents the presence of an interaction whereas white represents its absence. In the resampled network, each cell is shaded according to the probability that the interaction appeared in the resampled networks, with the colours as indicated in the colorbar at right.

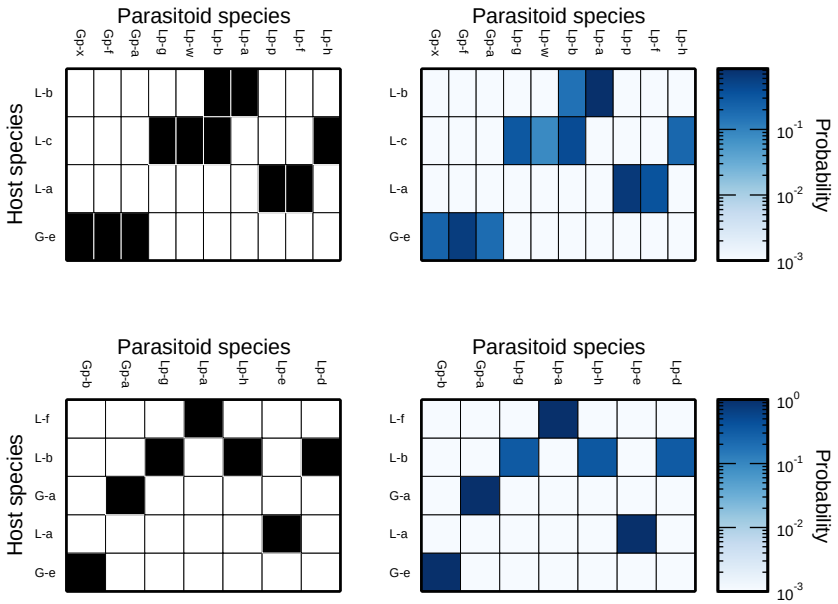


Figure 29: Graphical representation of the qualitative interaction network (left) and the mean of all 999 resampled networks (right) for site 13 in 2006 (top) and 2007 (bottom). Each cell represents a possible interaction between a host species and parasitoid species. In the qualitative network, a black cell represents the presence of an interaction whereas white represents its absence. In the resampled network, each cell is shaded according to the probability that the interaction appeared in the resampled networks, with the colours as indicated in the colorbar at right.

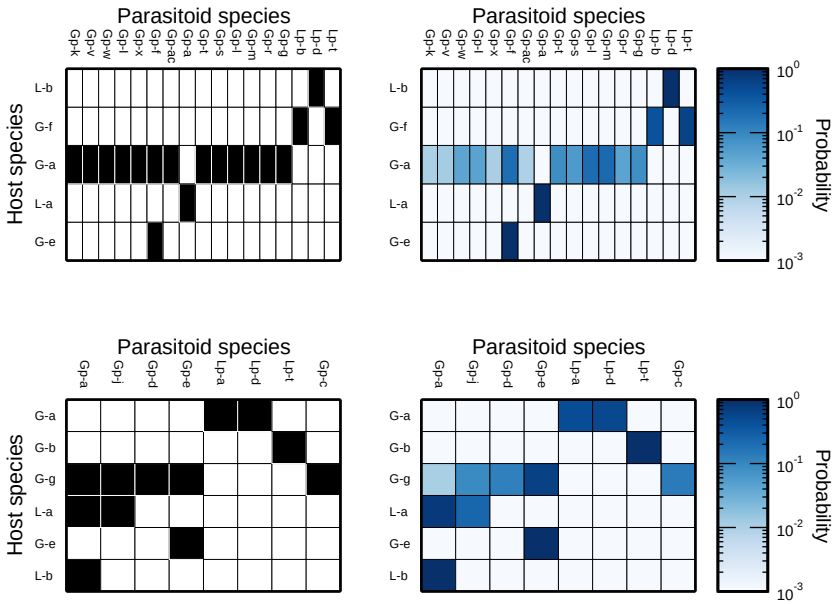


Figure 30: Graphical representation of the qualitative interaction network (left) and the mean of all 999 resampled networks (right) for site 14 in 2006 (top) and 2007 (bottom). Each cell represents a possible interaction between a host species and parasitoid species. In the qualitative network, a black cell represents the presence of an interaction whereas white represents its absence. In the resampled network, each cell is shaded according to the probability that the interaction appeared in the resampled networks, with the colours as indicated in the colorbar at right.

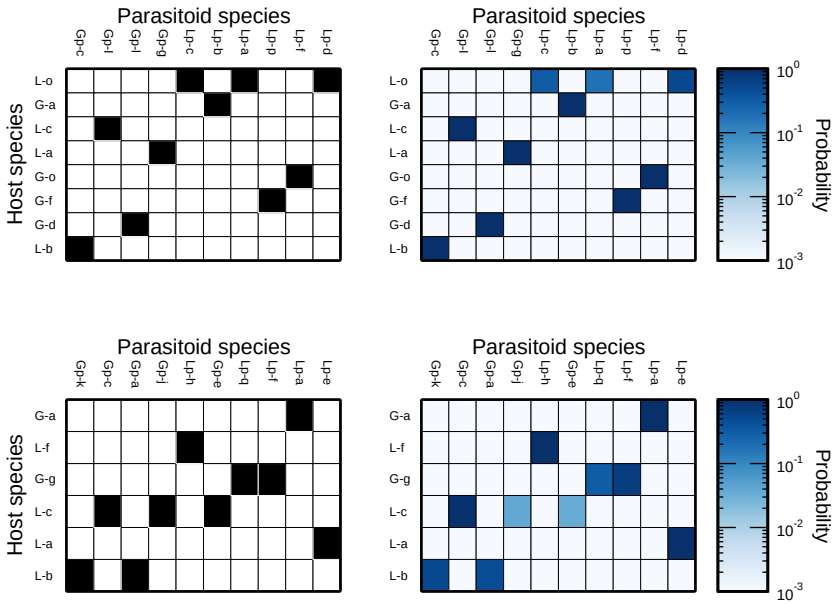


Figure 31: Graphical representation of the qualitative interaction network (left) and the mean of all 999 resampled networks (right) for site 15 in 2006 (top) and 2007 (bottom). Each cell represents a possible interaction between a host species and parasitoid species. In the qualitative network, a black cell represents the presence of an interaction whereas white represents its absence. In the resampled network, each cell is shaded according to the probability that the interaction appeared in the resampled networks, with the colours as indicated in the colorbar at right.

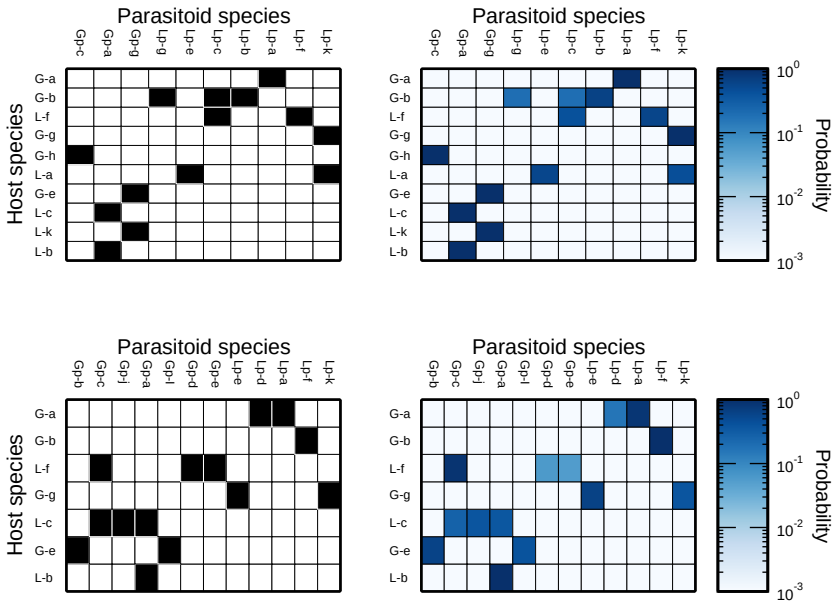


Figure 32: Graphical representation of the qualitative interaction network (left) and the mean of all 999 resampled networks (right) for site 16 in 2006 (top) and 2007 (bottom). Each cell represents a possible interaction between a host species and parasitoid species. In the qualitative network, a black cell represents the presence of an interaction whereas white represents its absence. In the resampled network, each cell is shaded according to the probability that the interaction appeared in the resampled networks, with the colours as indicated in the colorbar at right.

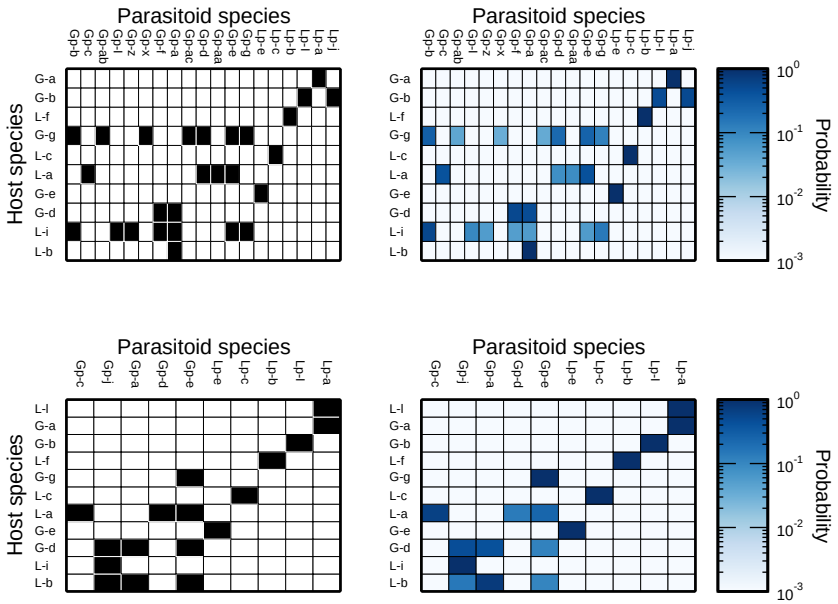


Figure 33: Graphical representation of the qualitative interaction network (left) and the mean of all 999 resampled networks (right) for site 17 in 2006 (top) and 2007 (bottom). Each cell represents a possible interaction between a host species and parasitoid species. In the qualitative network, a black cell represents the presence of an interaction whereas white represents its absence. In the resampled network, each cell is shaded according to the probability that the interaction appeared in the resampled networks, with the colours as indicated in the colorbar at right.

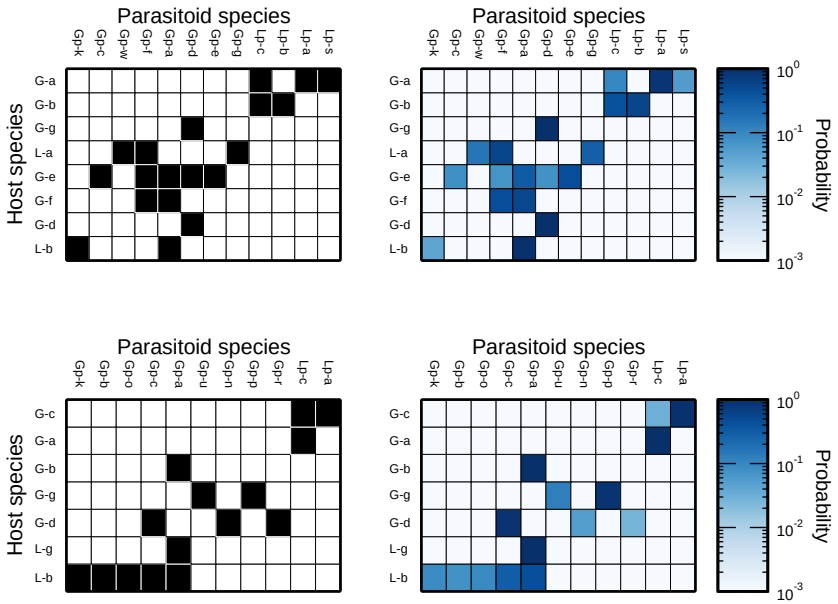


Figure 34: Graphical representation of the qualitative interaction network (left) and the mean of all 999 resampled networks (right) for site 18 in 2006 (top) and 2007 (bottom). Each cell represents a possible interaction between a host species and parasitoid species. In the qualitative network, a black cell represents the presence of an interaction whereas white represents its absence. In the resampled network, each cell is shaded according to the probability that the interaction appeared in the resampled networks, with the colours as indicated in the colorbar at right.

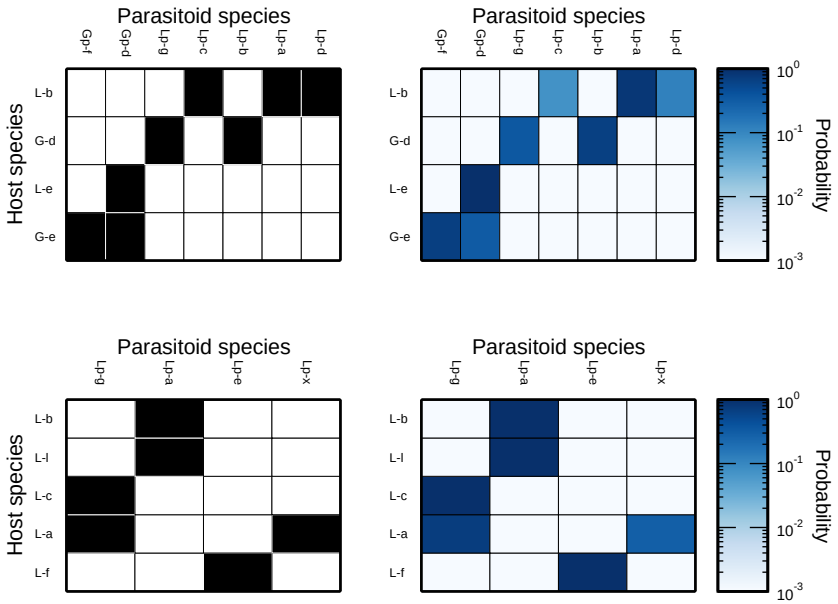


Figure 35: Graphical representation of the qualitative interaction network (left) and the mean of all 999 resampled networks (right) for site 19 in 2006 (top) and 2007 (bottom). Each cell represents a possible interaction between a host species and parasitoid species. In the qualitative network, a black cell represents the presence of an interaction whereas white represents its absence. In the resampled network, each cell is shaded according to the probability that the interaction appeared in the resampled networks, with the colours as indicated in the colorbar at right.

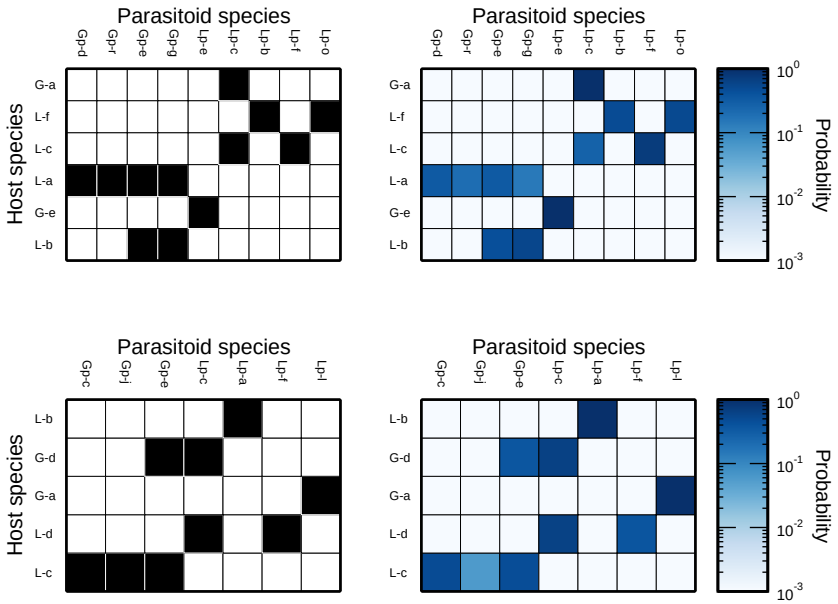


Figure 36: Graphical representation of the qualitative interaction network (left) and the mean of all 999 resampled networks (right) for site 20 in 2006 (top) and 2007 (bottom). Each cell represents a possible interaction between a host species and parasitoid species. In the qualitative network, a black cell represents the presence of an interaction whereas white represents its absence. In the resampled network, each cell is shaded according to the probability that the interaction appeared in the resampled networks, with the colours as indicated in the colorbar at right.

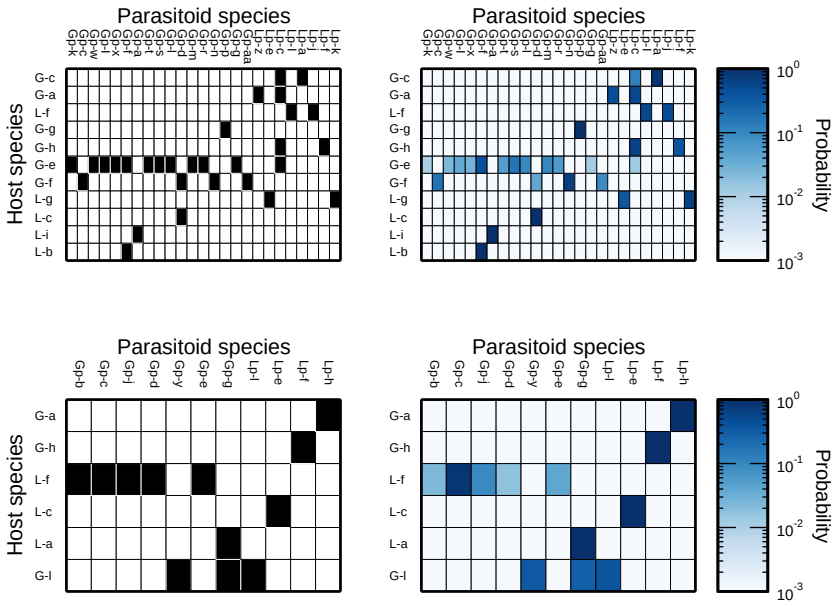


Figure 37: Graphical representation of the qualitative interaction network (left) and the mean of all 999 resampled networks (right) for site 21 in 2006 (top) and 2007 (bottom). Each cell represents a possible interaction between a host species and parasitoid species. In the qualitative network, a black cell represents the presence of an interaction whereas white represents its absence. In the resampled network, each cell is shaded according to the probability that the interaction appeared in the resampled networks, with the colours as indicated in the colorbar at right.

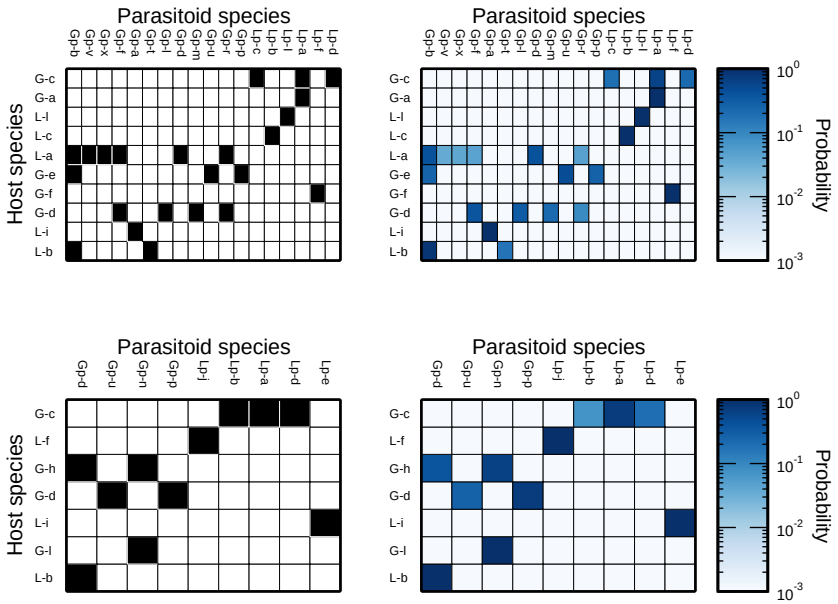


Figure 38: Graphical representation of the qualitative interaction network (left) and the mean of all 999 resampled networks (right) for site 22 in 2006 (top) and 2007 (bottom). Each cell represents a possible interaction between a host species and parasitoid species. In the qualitative network, a black cell represents the presence of an interaction whereas white represents its absence. In the resampled network, each cell is shaded according to the probability that the interaction appeared in the resampled networks, with the colours as indicated in the colorbar at right.

Results of network resampling – Role fidelity of hosts

When examining species fidelity of host roles, 2 out of 21 host species had significantly different measures of fidelity between the results for the qualitative networks and the resampling distributions (Fig. 39). Both species belonged to the galler feeding guild and both species showed no fidelity in the main text or in the resampling analysis. As a result, our conclusion from the main text that host species show fidelity of roles does not change since 8 out of 21 species continue to show fidelity.

For network fidelity of host roles, no networks had significantly different measures of fidelity between the results for the qualitative networks and the resampling distributions (Fig. 39). For temporal fidelity of host roles, no sites had significantly different measures of temporal fidelity between the qualitative networks and resampling distributions (Fig. 39)

Results of network resampling – Role fidelity of parasitoids

When examining species fidelity of parasitoid roles, 2 out of 49 parasitoid species had significantly different measures of fidelity between the qualitative networks and the resampling distributions (Fig. 40). Of these two species, the first (a leaf-miner parasitoid) showed no fidelity in the main text and variable fidelity in the resampling analysis. The second species (a galler parasitoid) showed fidelity in the main text but showed no role fidelity in the resampling analysis. If we were to reclassify the second species, which did not show fidelity in the resampling analysis, we would end up with 15 out of 49 species showing role fidelity. As this is still a statistically-significant proportion of parasitoids ($p < 0.001$), the conclusions from the main text about parasitoid species fidelity would not change.

For network fidelity of parasitoid roles, none of the networks had significantly different measures of fidelity between the qualitative networks and the resampling distributions (Fig. 40). For temporal fidelity of parasitoid roles, 6 out of 22 sites had significantly different measures of temporal fidelity between the qualitative networks and the resampling distribution (Fig. 40). Five sites showed highly variable measures of temporal fidelity in the resampling distributions. One site showed fidelity in the resampling analysis but did not in the main text. If we were to reclassify the site that changed in its measure

of temporal fidelity, we would still be left with 8 out of 22 sites where the the fidelity of parasitoid roles were significantly different between years ($p < 0.001$). Thus, the conclusions from the main text would not change.

Summary of network resampling

The fidelity of host roles at the species, network, and temporal levels did not change significantly between the qualitative networks and the networks in the resampling analysis. For parasitoid roles, there were a greater number of differences between the qualitative networks and the resampling results for species and temporal fidelity but not for network fidelity. Nevertheless, the conclusions from the main text about parasitoid species fidelity would not change as a result of statistical resampling. Overall, the results and conclusions presented in the main text appear robust to our use of qualitative interaction networks, despite the quantitative variation observed empirically.

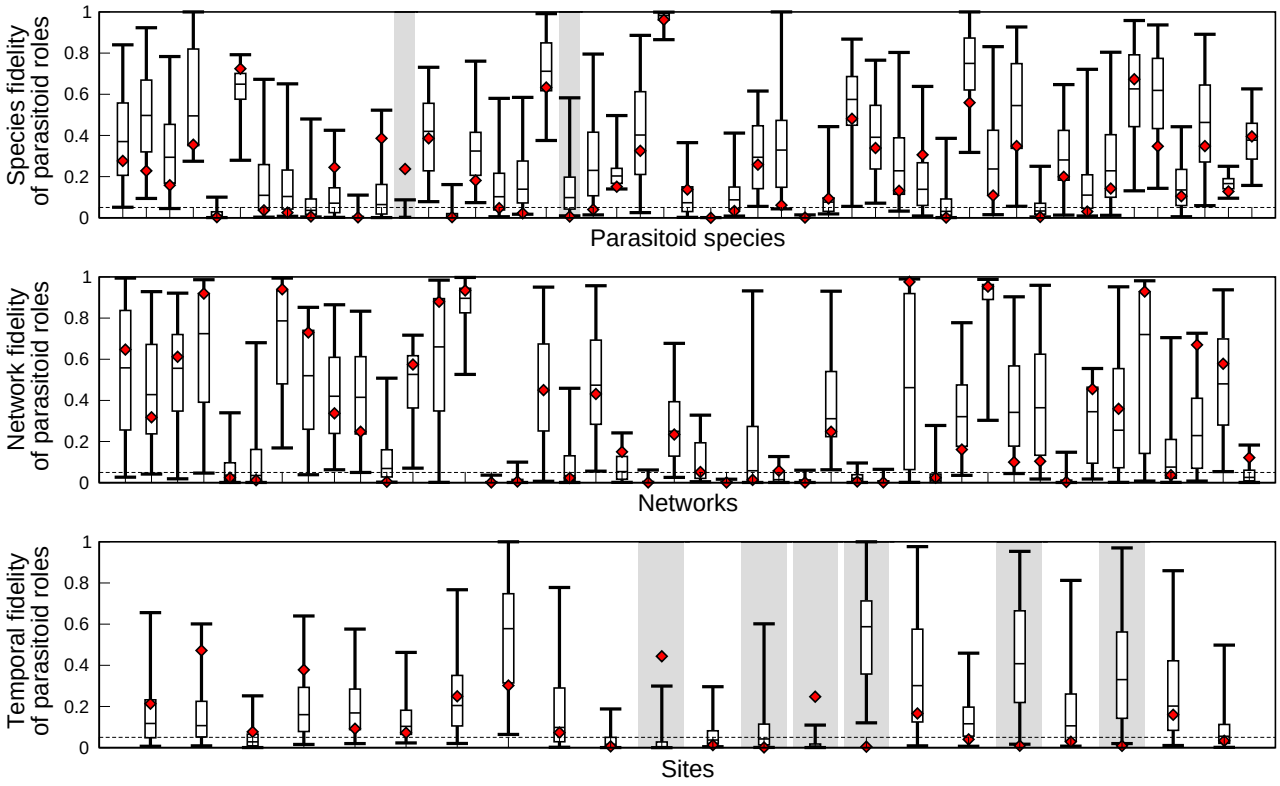


Figure 39: Comparison of role fidelity of hosts in the main text to the p-values for the resampled networks. From top to bottom, we show species fidelity, network fidelity, and temporal fidelity. Red diamonds show the fidelity values of the qualitative networks from the main text, while white boxes indicate the lower, median, and upper quartiles for the resampled data; the error bars show the 95% confidence intervals. Gray shading represents species, networks, or sites that showed significantly different measures of fidelity between the qualitative networks and the resampled networks.Values below the dotted line represent significant species and network fidelity and, in the case of temporal fidelity, represent sites that did *not* show fidelity between years.

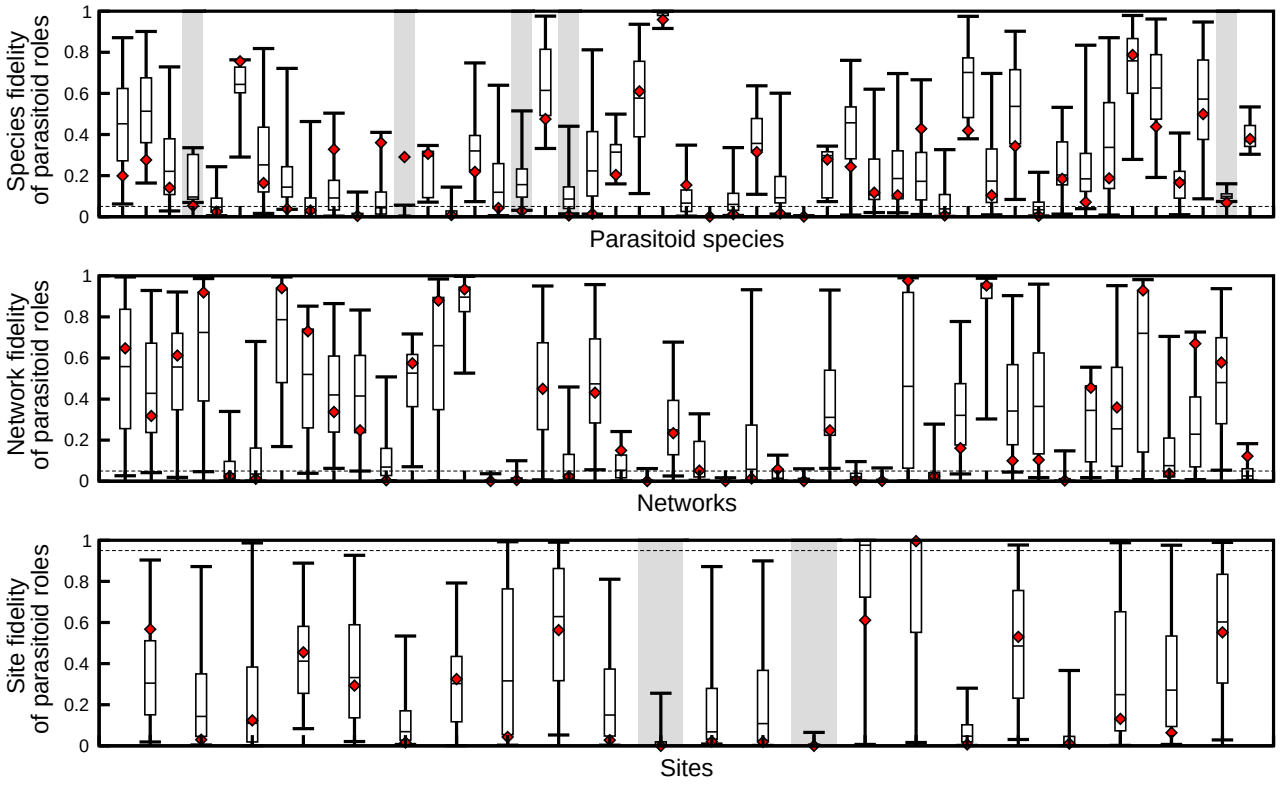


Figure 40: Comparison of role fidelity of parasitoids in the main text to the *p*-values for the resampled networks. From top to bottom, we show species fidelity, network fidelity, and temporal fidelity. Red diamonds show the fidelity values of the qualitative networks from the main text, while white boxes indicate the lower, median, and upper quartiles for the resampled data; the error bars show the 95% confidence intervals. Gray shading represents species, networks, or sites that showed significantly different measures of fidelity between the qualitative networks and the resampled networks. Values below the dotted line represent significant species and network fidelity and, in the case of temporal fidelity, represent sites that did *not* show fidelity between years.

Appendix 3

Bipartite network motifs

In our analyses, we calculated species' roles using motifs of size two to six. These motifs are represented in Figure 41.

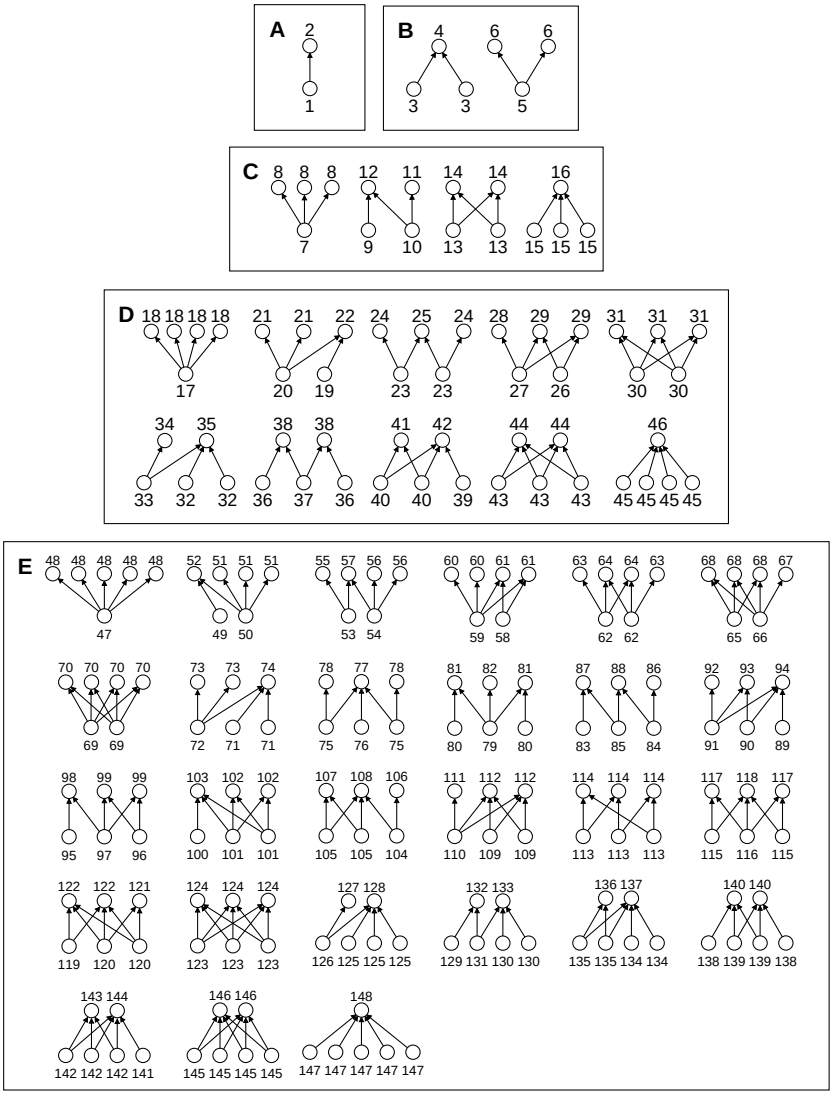


Figure 41: All bipartite motifs made up of (**A**) two, (**B**) three, (**C**) four, (**D**) five, and (**E**) six species. Circles represent species and the arrows represent interactions between species with direction of the arrows denoting energy transfer (e.g., from host to parasitoid). The different numbers indicate all of the uniquely-identifiable positions within each motif. In total, there are 44 motifs composed of 148 unique positions.

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